LINKING MORPHOLOGY AND PHYSIOLOGY AS PREDICTORS OF PRODUCTIVITY IN ELITE FAMILIES OF SOUTHERN PINES

A Dissertation

by

DANIEL JOZEF CHMURA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2008

Major Subject: Forestry

LINKING MORPHOLOGY AND PHYSIOLOGY AS PREDICTORS OF PRODUCTIVITY IN ELITE FAMILIES OF SOUTHERN PINES

A Dissertation

by

DANIEL JOZEF CHMURA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Approved by:

Chair of Committee,	Mark G. Tjoelker
Committee Members,	David D. Briske
	Tom D. Byram
	Wendell P. Cropper, Jr.
	Michael G. Messina
Department Head,	Steven G. Whisenant

May 2008

Major Subject: Forestry

ABSTRACT

Linking Morphology and Physiology as Predictors of Productivity

in Elite Families of Southern Pines. (May 2008)

Daniel Jozef Chmura, M.S., The August Cieszkowski Agricultural University of Poznan, Poland

Chair of Advisory Committee: Dr. Mark G. Tjoelker

Crown architecture affects tree growth through the control of leaf area and its display. Yet the linkages between crown structure, leaf traits, and productivity of elite selections of forest trees and responses to intensive silviculture are not fully understood. It was hypothesized that trees with crown and leaf traits governing efficient light capture and photosynthesis at the canopy scale would be the most productive. To this end, families of loblolly (*Pinus taeda*) and slash pine (*Pinus elliottii*) were grown at three experimental sites in the West Gulf Coastal Plain of Texas and Louisiana under two silvicultural treatments, including repeated fertilization with control of competing vegetation (HI), and a control (C) consisting of fertilization at planting.

Families and species differed in crown traits and aboveground productivity, and genotype differences increased throughout the first 5 years of stand development. Crown shape was important for light interception and growth initially, but at the onset of canopy closure, crown size, stand leaf area and its distribution within crowns affected canopy light interception and tree growth. Among all families and treatments, aboveground biomass productivity was positively related to absorbed photosynthetically active radiation (APAR) and canopy photosynthesis. Light-use efficiency (ε) varied from 0.41 to 0.56 g MJ^{-1} among families and was lowest in slash pine. Variability in aboveground biomass growth was related more to stand leaf area and APAR than to differences in light-use efficiency in these young stands. Leaf physiological, chemical and

morphological attributes changed within crowns in accordance with developing light availability gradients. Physiological attributes, such as net photosynthesis, were better predictors of family performance when integrated at the canopy level than leaf level in the examined pine species.

Crown size, light absorption, and aboveground growth generally ranked higher in the HI treatment than in the control, although the effects of the intensive silvicultural treatments did not differ statistically. Family performance was independent of treatment. Crown and canopy attributes, such as high leaf area index and large crowns with low leaf area density per crown volume, may be useful in the selection of highly productive genotypes of loblolly and slash pine under intensive silviculture.

ACKNOWLEDGMENTS

I thank the Department of Ecosystem Science and Management, the Forest Biology Research Cooperative and the Fulbright Program for financial support.

I thank my advisor, Dr. Mark G. Tjoelker for being a great teacher, for the wisdom and skills he shares with his students, and for all his help in my professional and personal life.

I want to acknowledge Dr. David D. Briske, Dr. Tom D. Byram, Dr. Wendell P. Cropper, Jr. and Dr. Michael G. Messina for serving on my Advisory Committee,

Dr. Belinda Medlyn for providing a revised version of the MAESTRA model and for help in modeling efforts,

Dr. Timothy A. Martin for providing unpublished results on photosynthetic parameters, and

Dr. Roma Żytkowiak and Tomas Martinez-Trinidad for help with methods on carbohydrates analyses.

I acknowledge and thank Dr. Mohd Rahman, Dr. Amir Hass, Tim Rogers, E.J. Billick, Corey Stover, Necdet Karakurt, Dave Dickson, Davis Buenger, Hsiao-Hsuang Wang (Rose) and Tomasz Koralewski for field assistance.

Most of all I thank my family. My wife, Agnieszka, provided me with constant support during my study. Our son, Jozef, is giving me joy and deepening the meaning of my life every day since he was born.

TABLE OF CONTENTS

Page

Page

Page

LIST OF FIGURES

FIGURE Page

FIGURE Page

LIST OF TABLES

TABLE Page

TABLE Page

NOMENCLATURE

Term	Explanation	Units
A_a	light-saturated photosynthetic rate on a leaf area basis	$\mu mol\ m^{-2}\ s^{-1}$
A_m	light-saturated photosynthetic rate on a leaf mass basis	$\mu mol\ g^{-1}\ s^{-1}$
A_{max}	leaf-level light-saturated photosynthetic rate	as above
aLAR	aboveground leaf area ratio – leaf area per aboveground biomass	$m^2\ kg^{-1}$
aLMF	aboveground leaf mass ratio – leaf mass per aboveground biomass	$g_{leaf}\ g^{-1}{}_{plant}$
APAR	absorbed photosynthetically active radiation	$MJ\ m^{-2}{}_{ground}$
BMD	branch mass density – branch mass per crown volume	$kg\ m^{-3}$
C	control treatment	none
$\delta^{13}C$	carbon isotope composition	‰
ε	light-use efficiency	$g\ MJ^{-1}$
J_{max}	light-saturated electron transport rate	$\mu mol\ m^{-2}\ s^{-1}$
N_a	area-based foliar nitrogen concentration	$g\ m^{-2}$
N_m	mass-based foliar nitrogen concentration	$mg\ g^{-1}$
HI	high intensity treatment	none
iPNUE	instantaneous photosynthetic nitrogen-use efficiency	$\mu mol\ mol\ N^{-1}s^{-1}$
LAD	leaf area density – projected leaf area per crown volume	$m^2\ m^{-3}$
LAI	leaf area index	$m^2{}_{leaf}\ m^{-2}{}_{ground}$
PAR	photosynthetically active radiation	$\mu mol\ m^{-2}\ s^{-1}$
PFD	photon flux density	$\mu mol\ m^{-2}\ s^{-1}$
SLA	specific leaf area	$cm^2\ g^{-1}$; $m^2\ kg^{-1}$
V_{cmax}	CO_2-saturated carboxylation rate	$\mu mol\ m^{-2}\ s^{-1}$
WUE	water-use efficiency	$mmol\ C\ mol^{-1}H_2O$

1. INTRODUCTION

Forest growth may be viewed as an outcome of physiological processes, allocational patterns and environmental conditions operating in the spatial and temporal settings of a stand of trees. In all photosynthesizing plants, carbon from the atmospheric CO_2 pool enters through a carbon-reduction cycle driven by the energy provided by light. Subsequently, it is used for synthesis of carbon compounds and is incorporated into plant biomass. Thus, plant growth is inherently related to CO_2 exchange. However, leaf-level photosynthetic rates usually only weakly correlate with plant growth, although the correlation is often stronger when photosynthesis is expressed on a leaf mass than leaf area basis (Poorter, 1989; Lambers et al., 1998; Reich, 1998). The difference between area- and mass-based correlations of leaf-level net photosynthesis rate with whole-plant growth rate underscores the importance of leaf morphology, particularly leaf area per unit leaf mass (specific leaf area – SLA), and whole-plant partitioning of biomass into leaves (leaf mass fraction – LMF, leaf dry mass per plant dry mass) in explaining differences in plant growth rates (Cornelissen et al., 1998; Reich, 1998). SLA and LMF together determine the leaf area ratio (LAR) – the amount of leaf area per total plant mass. In plant growth theory, LAR together with net assimilation rate (NAR – increase in plant mass per unit leaf area per unit time) determine relative growth rate - RGR (Poorter and Garnier, 1999). In broad comparisons among species that differ in growth rate, RGR is usually weakly correlated with NAR, whereas correlations with LAR, and especially with SLA are strong (Lambers et al., 1998), further underscoring the importance of leaf area in explaining differences in plant growth.

The importance of leaf area stems from its role in light interception and photosynthetic carbon gain. In forest canopies, light conditions vary considerably both spatially and temporally (Pearcy, 1990; Kimmins, 1997). Apart from the effects of the

---

This dissertation follows the style of Forest Ecology and Management.

overall light environment, such as sun zenith angle and the ratio of direct to diffuse radiation, the amount of light within a forest canopy is largely governed by the amount of leaf area and its distribution, which in turn is dependent upon crown architecture and canopy structure. On the other hand, crown architecture is influenced by a number of developmental and functional constraints that lead to characteristic crown shapes and leaf arrangement patterns (Pearcy et al., 2005).

In addition to canopy structure, leaves differ in morphological and physiological traits that are often arrayed along light-environment gradients. In this regard, acclimation (i.e. phenotypic plasticity) to the variable light environment of forest canopies is typically reflected in an increase of SLA with canopy depth, often facilitating light interception in the shaded conditions of lower crowns (Ellsworth and Reich, 1993; Niinemets and Kull, 1995). Foliar nitrogen concentration and leaf photosynthetic properties also change accordingly with light intensity, and these adjustments are hypothesized to maximize carbon gain at canopy level (Field, 1983; Hirose and Werger, 1987).

Given the within-crown variability in leaf morphological and physiological attributes, the canopy photosynthesis is not easily predicted from leaf-level properties. In order to scale to the canopy level, these modes of variability as well as complicated light interception patterns related to leaf arrangement and their spectral properties must be taken into account (Boote and Loomis, 1991). Accordingly, process-based models are invaluable as tools for scaling photosynthesis from the level of leaves to canopy (Norman, 1980; Norman, 1993). The Farquhar and von Caemmerer (1982) model of leaf photosynthesis based on photosynthetic biochemistry together with algorithms for light interception are widely used in modeling canopy carbon assimilation (Wang and Jarvis, 1990a; Evans and Farquhar, 1991; Norman and Arkebauer, 1991).

Most models of light interception assume that light attenuation within a canopy follows the Beer-Lambert law:

$$I_s = I_0 \exp(-kLAI) \qquad (1.1)$$

where: I_s is the quantum flux density at height s in the canopy, I_0 is the flux density at the top of the canopy, k is a light extinction coefficient and LAI is a cumulative leaf area index above the point s. Using this law requires an assumption of random distribution of leaf area, which is rarely true in forest canopies where foliage is aggregated to varying degrees. Empirical studies confirmed the suitability of the law for describing light environments in forest canopies (Pierce and Running, 1988; Vose et al., 1995). However, especially in conifer stands the use of the Beer-Lambert law may require some modifications to account for foliage clustering in crowns and shoots within crowns (Gholz et al., 1991). Norman and Welles (1983) developed a radiative transfer model suitable for description of light penetration in a wide array of canopy structures ranging from widely-spaced plants to full cover. This model serves as the basis of a light-interception procedure in a process-based model of canopy light absorption and photosynthesis – MAESTRA (Medlyn, 1998), used in this dissertation.

The relationship between plant growth and intercepted light is often linear, which has lead to the concept of light-use efficiency (Monteith, 1977), defined as the slope (ε) of the relationship between intercepted or absorbed PAR (photosynthetically active radiation) and biomass growth. Linear relationships between intercepted light and aboveground biomass growth have been reported in trees (Cannell, 1989; Dalla-Tea and Jokela, 1991), despite the fact that instantaneous leaf-level photosynthesis is not linearly related to light intensity. Integration from leaf to canopy scale and from instantaneous to longer time scales tends to linearize the intercepted light vs. plant growth relationship (Stenberg *et al.*, 1994; Medlyn, 1998). However, other hypotheses concerning the linear response of biomass growth to absorbed PAR have been advanced, including relating light-use efficiency to within-crown foliar nitrogen distribution and optimization of canopy photosynthesis (Dewar, 1996; Haxeltine and Prentice, 1996). Although simple in principle, light-use efficiency is likely complex in its underpinnings, involving the efficiency of light capture, rates of photosynthesis, and the efficiency of conversion of photosynthates into biomass. In the practice of forestry, aboveground, and especially

stemwood biomass is of paramount interest. Therefore, in this context growth efficiency also involves biomass allocation patterns.

Loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) are two species native to the Southeastern United States. Although the natural range of slash pine is much smaller than that of loblolly pine, these two species are the most important commercially among southern pines and are widely planted throughout the region. Slash pine is usually recommended over loblolly pine for planting on wetter sites (Shoulders and Tiarks, 1980; Schultz, 1997). However, on many sites the productivity of loblolly pine is equal to or greater than that of slash pine, especially in intensively managed forest plantations (Colbert et al., 1990; Jokela and Martin, 2000; Shiver, 2002). In addition, genotypes within both loblolly and slash pine differ in aboveground biomass productivity (McCrady and Jokela, 1996; 1998; Lopez-Upton et al., 2000; Roth et al., 2007), but the linkages of growth with morphological and physiological attributes are not well resolved. Currently, most planting material originates from breeding programs that utilize genetic variation for improved growth and health of forest plantations (McKeand et al., 2003). In pine forests of the Southeastern United States, leaf area is viewed as one of the major factors governing forest productivity (Allen et al., 2005). However, on many sites throughout the region, water (both excess and shortage) and nutrient availability are limiting leaf area development and potential forest growth (Allen *et al.*, 1990; Albaugh *et al.*, 1998; Allen *et al.*, 2005). Thus, the potential remains to increase forest productivity by the deployment of highly productive genotypes coupled with manipulation of site resources.

The main objective of my study was to examine whether and how morphological and physiological traits are interrelated in determining differences in aboveground productivity among selected genotypes of loblolly and slash pine. It was hypothesized that the most productive genotypes will exhibit a suite of traits favorable for increased light interception and aboveground growth. Of interest was a comparison of the effects of genotype, silvicultural treatment and their possible interactions on crown structural

and leaf morphological and physiological properties, and aboveground biomass growth in intensively managed forest plantations.

The specific objectives of my study were to:

- Determine species or family-specific allocation patterns that lead to differences in productivity in young stands. It was hypothesized that trees with a high leaf mass fraction (LMF) and especially with a high leaf area ratio (LAR) would have greater growth.
- Establish which crown and canopy characteristics, e.g. crown shape, crown volume, leaf area and its distribution, are underpinning differences in aboveground productivity among selected genotypes. It was expected that trees with larger crowns and greater total leaf area would intercept more light and grow more.
- Determine whether within-crown leaf physiological and morphological attributes provide the insight into differences in aboveground growth performance. It was hypothesized that families with the highest photosynthetic rates and the most plastic response of leaf morphology and physiology to light availability gradients within crowns would show the greatest productivity.
- Determine resource-use efficiency (light, nutrients and water) among selected families of southern pines. It was expected that families showing the highest light- and nitrogen-use efficiency would exhibit increased growth. On the other hand, it was expected that increased water-use efficiency would not confer a growth advantage, especially in the high-intensity silvicultural treatment.
- Examine whether and how intensive silvicultural treatment, consisting of regular fertilization and control of competing vegetation, affect crown and canopy characteristics or physiological traits important for stand productivity, and whether and how selected families differ in response to silvicultural treatments in the study area of the West Gulf Coastal Plain of east Texas and Louisiana. It was hypothesized that improved nutrition will lead to increases in leaf area and aboveground growth.

The second section of the dissertation addresses the effects of differences in crown shape and structure and biomass allocation patterns on aboveground growth in the

examined pine species and families. The third section focuses on within-crown variability of leaf morphology, chemistry and physiology that affect canopy photosynthesis. The fourth section addresses the effects of crown size, leaf area and its distribution on light-use efficiency with the use of the MAESTRA model for estimating canopy light absorption and photosynthesis. Four appendices provide supporting supplemental information. Appendix A presents the results of within-crown variability of total non-structural carbohydrates in the examined families. Appendix B reports a study of water-use efficiency, using stable carbon isotopes. Appendix C reports allometry coefficients and physiological parameters used in the simulations of canopy light absorption and photosynthesis described in Section 4. Appendix D documents crown profile shapes at the onset of canopy closure in the studied families of southern pines.

In general, family and species differed in crown traits and aboveground productivity and genotype differences increased throughout the first 5 years of stand development. Imposed silvicultural treatments did not significantly affect the examined traits, although trees were larger and grew faster in the high intensity than in the control treatment. Crown shape was important for light interception and growth before canopy closure, but crown size, stand leaf area and its distribution within crowns affected canopy light interception and tree growth at the onset of canopy closure. Families differed in light-use efficiency and crown and stand attributes, such as leaf area index (LAI), affecting ε and productivity. In order to link physiological traits with tree growth and forest productivity, leaf-level physiology should be integrated to crown and canopy levels. The results of this dissertation will help in guiding the selection criteria for the most productive ideotypes (Martin et al., 2001) in the examined pine species under intensive silviculture.

2. CROWN STRUCTURE AND BIOMASS ALLOCATION PATTERNS MODULATE ABOVEGROUND PRODUCTIVITY IN YOUNG LOBLOLLY PINE AND SLASH PINE*

2.1. Overview

Crown architecture affects tree growth through control of leaf area and its display for effective light capture and photosynthesis. It may be important to quantify crown traits for effective use of intensive silvicultural practices to improve tree growth in forest plantations. We examined growth and crown characteristics in two families of loblolly pine (*Pinus taeda* L.) with contrasting growth - superior and average, and one slash pine (*Pinus elliottii* Engelm.) family, growing at three experimental sites in the West Gulf Coastal Plain of Texas and Louisiana, USA. The families were subjected to two contrasting silvicultural treatments – repeated fertilization and control of competing vegetation (high intensity), and control (low intensity). Families differed in height and diameter growth after the second growing period in the field, and high intensity treatment in general increased tree growth, although family ranks and silvicultural effects were dependent on the experimental site. The families differed in crown and needle traits, and biomass partitioning patterns. Aboveground biomass accumulation was related to crown structure among families, but biomass partitioning was independent of the crown traits. Cultural treatment generally had no effect on crown properties or aboveground biomass partitioning. Slash pine produced significantly smaller crowns than loblolly pine at a given tree size, but was capable of maintaining larger needle area and producing more bole-wood biomass for a given crown volume. Tree growth was highly correlated with accumulated foliage area, but bole-wood production per unit leaf

* Reprinted with permission from "Crown structure and biomass allocation patterns modulate aboveground productivity in young loblolly pine and slash pine" by Daniel J. Chmura, Mohd S. Rahman and Mark G. Tjoelker, 2007, For. Ecol. Manage, 243, 219 – 230, Copyright [2007] by Elsevier B.V.

area (growth efficiency) was similar for both pine species. The superior loblolly pine family had the largest number of flushes and a different crown shape than two other families that most likely led to better light-capture and greater carbon assimilation, as this family also produced the greatest aboveground biomass.

2.2. Introduction

Tree growth reflects the interdependence of physiological processes, biomass allocation patterns and growth rates as influenced by the inherent genetic background of the individuals and the environment in which the individuals are grown. Spatial and temporal integration of these processes determines stand-level production, expressed either as accumulated carbon, biomass, or wood production (Will et al., 2001; Chapin et al., 2002; Martin et al., 2005).

In the Southeastern United States, loblolly pine and slash pine are the main softwood timber species. The natural geographic range of slash pine is smaller than that of loblolly pine, but both species are widely planted throughout the South. Genetic variability lies at the basis of tree breeding programs aimed at increasing forest productivity and providing a sustainable supply of timber products (McKeand et al., 2003). Although practically all seedlings of both species planted in commercial forest plantations in the region come from genetically improved sources (McKeand et al., 2003), the potential remains to increase productivity through the use of best-performing genotypes. However, the deployment of genetically improved planting material should be coupled with appropriate silvicultural practices to obtain the best possible returns from resources invested in the establishment and maintenance of forest sites.

Loblolly and slash pine differ in aboveground biomass productivity and in growth response to intensive silvicultural treatments (Colbert et al., 1990; Jokela and Martin, 2000; Xiao et al., 2003a; Martin and Jokela, 2004b). Also genotypes within both species differ in growth and biomass accumulation (McCrady and Jokela, 1996; 1998; Lopez-Upton et al., 2000; Roberts, 2002; McKeand et al., 2006; Roth et al., 2007), but the exact causes of this variability remain unknown.

Although growth differences in plants may result from variation in rates of carbon gain, the published results regarding differences in leaf-level net photosynthesis between loblolly and slash pine are mixed. Will et al. (2001) found no significant differences in leaf-level photosynthesis rates between slash and loblolly pine. In contrast, McGarvey et al. (2004) reported about 14% higher leaf-level area-based photosynthetic rates for slash than for loblolly pine; however, when integrated for the whole tree, total canopy photosynthesis was slightly higher for loblolly than for slash pine. Consequently, differences in productivity between loblolly and slash pine have been proposed to arise largely from variation in accumulated leaf area, rather than from different leaf-level photosynthetic rates (Will et al., 2001; McGarvey et al., 2004).

The lack of obvious between-species differences in leaf-level photosynthesis and the close link of tree productivity with leaf area imply that species- or genotype-specific differences in crown structure and leaf biomass allocation patterns might modify tree growth and productivity. The spatial distribution of leaf area and biomass within a crown might control light interception and influence net CO_2 exchange rates at the whole tree and stand levels (Wang and Jarvis, 1990b). Different leaf area or leaf biomass distributions within crowns have been reported among families of loblolly pine (McCrady and Jokela, 1996; 1998) and between loblolly and slash pine (Xiao et al., 2003a). Fertilization only or applied with thinning had no effect on vertical leaf area distribution in loblolly pine stands 9-14 years of age (Vose, 1988; Gillespie et al., 1994). A positive relationship of aboveground growth and leaf area index (LAI – m^2 leaf area m^{-2} ground area) has been reported in 4 to 18-year-old stands of both loblolly and slash pine, independent of management intensity (McCrady and Jokela, 1998; Jokela and Martin, 2000; Borders et al., 2004; Martin and Jokela, 2004a; Samuelson et al., 2004; Will et al., 2005), suggesting that the development and maintenance of leaf area in a forest plantation is an important determinant of productivity. However, little is known about family- or species-specific responses to various silvicultural practices in terms of crown structure and its consequences for biomass productivity.

Currently most industrially managed forest plantations in the South utilize intensive treatments to alleviate nutrient and water limitations (Allen et al., 2005). The most common practices include fertilization and control of competing vegetation. Results from seven long-term experiments summarized by Jokela et al. (2004) confirm the effectiveness of these treatments in enhancing stem-wood biomass production in loblolly pine; they are also successful in slash pine plantations (Jokela and Martin, 2000; Martin and Jokela, 2004b) However, as suggested by Xiao et al. (2003b), nutrient demands for growth might be dependent on the genotype of these species. Therefore, it is important to examine both the effect of silvicultural practices and their interactions with species and/or genotype on growth performance in forest plantations.
In this paper we investigate variability in aboveground biomass accumulation in selected families of loblolly and slash pine growing in replicated experiments under two contrasting silvicultural intensities in the West Gulf Coastal Plain area in Texas and Louisiana. Our specific objectives were to i) determine relative differences in accumulated aboveground biomass; ii) establish whether and how crown characteristics are linked to differences in productivity and biomass allocation patterns in the examined families; iii) determine how the above-mentioned relationships are affected by silvicultural management intensity.

2.3. Materials and Methods

2.3.1. Experimental sites

The West Gulf series of the PPINES (Pine Productivity Interactions on Experimental Sites) experiment consists of three sites: Kirbyville, Texas (30º 35' N, 93º 59' W); DeRidder, Louisiana (30º 51' N, 93º 21' W); and Bogalusa, Louisiana (30º 52' N, 89º 51' W). The study is a part of the Forest Biology Research Cooperative coordinated by the University of Florida. The Bogalusa site is located in the East Gulf Coastal Plain area and two other sites are located in the West Gulf Coastal Plain, but together are hereafter referred to as West Gulf Coastal Plain sites. Hot and humid summers and mild

winters characterize the climate of this region (Table 2.1). The sites differ in their soil drainage classification and texture in the surface and sub-surface layers. The Kirbyville site is a moderately well drained site, DeRidder is a somewhat poorly drained site and Bogalusa is a poorly drained site. Both DeRidder and Bogalusa have a silt loam surface and sub-surface soil texture, while Kirbyville has a fine sandy loam surface soil and sandy clay loam sub-surface soil.

Table 2.1. Long-term (1971 – 2000) mean values of climatic data[1)] for each of three experimental sites in the West Gulf Coastal Plain area.

		Temperature [°C]			Precipitation sum
Site		average	max.	min.	[mm]
Bogalusa, LA	Annual	19.2	25.4	12.9	1627
	January	9.6	15.7	3.5	157
	July	27.8	33.4	22.1	144
DeRidder, LA	Annual	19.3	25.3	14.4	1560
	January	9.3	15.2	3.3	160
	July	27.8	32.7	22.9	133
Kirbyville, TX[2)]	Annual	19.2	25.1	13.2	1399
	January	9.3	15.1	3.5	149
	July	27.7	33.4	22.0	94

[1)]From the nearest recording station, NOAA National Oceanic and Atmospheric Administration. [2)]Town Bluff Dam, Texas.

The experiment was established using a split-plot design. Two contrasting silvicultural treatments - control (C) and high intensity (HI) were assigned as a main-plot factor. Both treatments at all three sites were sprayed with Arsenal® (imazapyr) and Garlon™ (triclopyr) before planting to control the herbaceous and woody vegetation, and fertilized with 280.5 kg ha^{-1} of diammonium phosphate (50.5 kg ha^{-1} N and 55.5 kg ha^{-1} P) at the time of planting. Starting with the second growing season, the two cultural treatments varied; HI received control of competing vegetation yearly (until canopy closure) and regular fertilization based on yearly analyses of foliar nutrient concentrations, whereas C did not receive any further fertilization or weed control. Cumulative rates of nutrients applied throughout the two growing seasons in the HI

treatment reached 163 and 67 kg ha^{-1} for N and P, respectively at Bogalusa and DeRidder, and 105 and 116 kg ha^{-1} at Kirbyville. K fertilization was applied only at Bogalusa and DeRidder at 45 and 38 kg ha^{-1}, respectively. Mg, S, and B were applied only at Bogalusa at 22.4, 44.9, and 0.56 kg ha^{-1}, respectively. At the end of the second growing season, foliar nutrient concentrations in the HI treatment were on average higher by 43% for N and 32% for K, and lower by 6% for P than in the C treatment. S, B, and Mn foliar concentrations were 29%, 50%, and 12% higher in HI than in C, respectively. Concentrations of other microelements did not differ between the two cultural treatments. All sites received monthly tip moth (*Rhyacionia* spp.) control with Mimic™ (tebufenozide) during the first growing season.

Five elite full-sib families of loblolly pine, one poorer-growing loblolly pine family and one elite family of slash pine were assigned as sub-plots within cultural treatments. Four of the loblolly pine families originated from SE Texas, one from Livingston Parish, LA, and one from the Atlantic Coastal Plain area (superior loblolly). The slash pine family originated from the West Gulf area. The experimental sites were established between November 2001 and January 2002. Each site was prepared by plowing beds prior to planting. Seedlings were raised in 66 ml Ray Leach "Cone-tainer"™ cells (Stuewe & Sons, Inc. Corvallis, Oregon, USA) in 2001 and out planted in 2.4 × 3.3 m spacings (1,223 trees ha^{-1}) in 0.0588 ha pure-family plots. An additional plot with a proportional mixture of all seven families was included in each cultural treatment main-plot to be used for destructive harvests. There were 72 trees (eight beds × nine trees) in each individual sub-plot, with the inner 42 trees designated as the measurement plot. The treatment design was replicated in five complete blocks at each site. Cultural treatment main-plots were separated by eight rows of buffer trees within a block.

2.3.2. Measurements

Growth analysis was based on the stand inventory data - tree height and diameter at 1.3 m (DBH) - collected for all families in the experiment at the end of the second

annual growing period. Tree volume index ($DBH^2 \times$ height, dm^3) was used in the analysis as it integrates both measured traits in a single variable.

Three out of seven families were selected for study of allometric relationships and crown traits. Two loblolly pine families were chosen based on their average and superior growth performance in the first year; therefore, they will hereafter be referred to as average and superior. Slash pine (slash) was included to allow between-species comparisons.

During the dormant season after the second growing period in the field, in November 2003, 24 trees (4 trees / 3 families / 2 cultural treatments) were destructively harvested from mixed-family plots at each of three experimental sites to develop species-specific biomass allometric equations. Trees within particular family and cultural treatment combinations were selected to represent the entire tree diameter range. Tree height of the sampled trees ranged from 1.81 to 3.92 m in the loblolly pine families and from 1.85 to 2.90 m in the slash pine family. The corresponding range of DBH values was from 1.58 to 6.02 cm for loblolly pine trees and 2.71 to 5.35 cm for slash pine.

In total we sampled 72 trees, which were of good form and free of any visible defect (gall, canker, needle rust, etc.). The entire aboveground portion of each tree was separated into components – foliage, branches, and bole, and transported to the laboratory for further analysis. All samples were oven-dried at 65 °C and weighed to the nearest 0.1 g. At harvest, needles from the last flush with fully elongated needles were collected along the crowns to determine specific leaf area (SLA, cm^2 leaf area g^{-1} leaf dry mass). All-sided SLA was determined on a random sub-sample of 20 needle fascicles from each tree, using a water volume displacement method (Johnson, 1984). Total leaf area (all-sided) per tree was obtained by multiplying total foliage dry mass by corresponding SLA. Since our estimates of leaf area ratio (LAR - the amount of leaf area per total plant mass) and leaf mass fraction (LMF - leaf dry mass per plant dry mass) are calculated on the aboveground portion of the tree, the reported values are further referred to as aboveground leaf area ratio (aLAR) and aboveground leaf mass fraction (aLMF).

The same harvested trees were used to investigate crown architecture. On each tree we measured total height, DBH and lengths of individual internodes. In each whorl we measured branch angle and the lengths of two opposing branches. To obtain crown volume, we calculated the mean values of branch length and branch angle for each whorl within the tree. Based on the coefficient of variation (CV) of the two measurements for the same node, we assumed that crowns were symmetrical. Most of the CV values were less than 9% for branch angle and 18% for branch length. We assumed that branches were straight and that their inclination to the stem was uniform along the entire branch length. Thus, in our model, a right triangle was formed by a branch (hypotenuse), together with the distance between branch tip and tree trunk, and the distance between the whorl and the projection of the branch tip on the tree trunk, measured along the bole. From the branch length (hypotenuse) and the sine and cosine of branch angle we were able to calculate the distance of the branch tip from the tree trunk and the height of resulting triangle. This method enabled us to construct a spatial model of the crown of each individual tree, which is composed of two cones (bottom - created by the branches of the first live whorl, and top - connecting the tips of branches of last whorl with the tree top) and several conical frusta. We did not exclude the inner, defoliated part of a crown from the crown volume. Other studies on loblolly pine crowns have shown that this portion of the crown is relatively small (Baldwin and Peterson, 1997), ranging from 3 to 4% of crown volume in loblolly pine trees between 10 and 40 years of age (Baldwin et al., 1998).

2.3.3. Analysis

The stand inventory data for all seven families were subject to analysis of variance (ANOVA) separately for each experimental site and subsequently for all three sites together, based on average plot values of volume index at age 2 years for family within cultural treatment. Mixed-family plots were excluded from the analysis. Moreover, one replication (block) was excluded from analysis at DeRidder due to lack

of measurement data, and one at Bogalusa, because of poor survival and growth as a result of flooding in low-lying depressions. Across all sites, survival rate was satisfactory in the other replications, with survival higher than 90% on the majority (78%) of plots (mean survival = 92%, range 55 to 100%).

Because of the requirements for the allometric study, trees were not randomly selected, but rather were chosen across a range of sizes within each family. Therefore, to account for size variation among our sample trees, we used analysis of covariance (ANCOVA), with tree diameter (DBH) as a covariate in the analysis of crown-related traits and aboveground biomass partitioning. To analyze the relationship of crown traits with leaf area and partitioning of biomass to different aboveground components, we used crown volume as a covariate, as it represents the composite of different crown traits and its correlations with all biomass components were highest. Initially, a full model with separate slopes was fit to the data for each site with the following general equation:

$$Y_{ijk} = \mu + C_i + F_j + CF_{ij} + \mathrm{Cov} + F_j\,\mathrm{Cov} + e_{ijk} \qquad (2.1)$$

were Y_{ijk} is the examined variable on the k^{th} tree in j^{th} family and i^{th} cultural treatment (i = 1, 2 ; j = 1, 2, 3; k = 1, 2, 3, 4), C_i is the fixed effect of i^{th} cultural treatment, F_j is the fixed effect of j^{th} family, Cov is a covariate variable (DBH or crown volume) and e_{ijk} is the random error. In the case of equality of slopes, a test for equality of least squares means was conducted on the reduced model with equal slopes, which is specified by the equation 2.1 without the F_jCov term.

We used Type I regression analysis to study the relationships of crown and growth traits. Individual data were logarithmically (ln) transformed when necessary to ensure the normality of distribution and homogeneity of variances (Ott and Longnecker, 2001). Comparisons of means or least squares means were made using the Tukey-Kramer HSD test. Between-species differences and cultural treatment differences were tested using contrast analysis. All analyses were conducted with JMP 5.0.1 statistical software (SAS Institute Inc., Cary, NC, USA).

2.4. Results

2.4.1. Tree growth

Stand inventory data revealed that volume index differed among the seven examined genotypes at all experimental sites ($P \leq 0.0074$). The superior loblolly pine family had the largest trees, except at Bogalusa (Table 2.2), where the slash pine family had the highest volume index, reflecting changes in family ranking among sites (family × site effect, $P = 0.0045$, Table 2.2).

Intensive cultural treatment through the second growing season in the field, in general, increased tree growth in all families. However, the effect of combined fertilization and weed control on tree growth was significant only at the Kirbyville site ($P = 0.0036$), where volume index was increased on average by 58% compared to the control. Although volume index was higher under the HI treatment compared to the control at the remaining two sites (Table 2.2), this effect was not statistically significant. Generally, the effects of genotype and cultural treatment were independent, as indicated by the lack of family × treatment interaction effects.

2.4.2. Crown traits

At the end of the second year, the two selected loblolly pine families had a significantly greater ($P < 0.05$) cumulative number of flushes (on average 10 and 11 internodes for the average and superior families, respectively) than the slash pine family (six internodes), and silvicultural treatment did not affect that trait at any experiment location (data not shown). The average loblolly pine family had more open branch angles than the slash pine family ($P < 0.05$) at two of the three sites, except at Kirbyville. However, branch angles when compared at the same relative height within a crown, generally varied little among the examined families (Figure 2.1) and cultural treatments.

Table 2.2. Average values and 95% confidence intervals of tree volume index ($DBH^2 \times Ht$, dm^3) for examined families of loblolly pine and slash pine after the second growing season in two contrasting cultural regimes at three experimental sites.

Bogalusa				DeRidder				Kirbyville			
Family	**Volume index**			**Family**	**Volume index**			**Family**	**Volume index**		
	[dm^3]		**95% C.I.**		**[dm^3]**		**95% C.I.**		**[dm^3]**		**95% C.I.**
slash[1)]	2.43	a	1.69 - 3.50	sup. lob	2.61	a	1.82 - 3.75	sup. lob	9.93	a	8.74 - 11.27
sup. lob	2.29	a	1.59 - 3.30	lob. 4	2.17	ab	1.60 - 2.95	aver. lob	7.85	ab	6.91 - 8.92
lob. 4	1.60	ab	1.11 - 2.31	lob. 3	2.11	ab	1.56 - 2.87	lob. 4	7.31	b	6.43 - 8.30
lob. 3	1.36	ab	0.95 - 1.97	aver. lob	2.05	ab	1.51 - 2.78	lob. 3	6.91	bc	6.08 - 7.85
lob. 2	1.14	ab	0.79 - 1.65	lob. 2	1.49	ab	1.10 - 2.03	lob. 2	5.40	c	4.75 - 6.13
aver. lob	1.03	b	0.71 - 1.48	slash	1.45	ab	1.06 - 1.96	slash	5.32	c	4.68 - 6.04
lob. 7	0.89	b	0.62 - 1.29	lob. 7	1.12	b	0.82 - 1.52	lob. 7	3.53	d	3.11 - 4.01
Treatment				**Treatment**				**Treatment**			
HI[2)]	2.07	a	1.07 - 3.98	HI	2.05	a	1.60 - 2.62	HI	7.93	a	6.85 - 9.17
C	1.00	a	0.52 - 1.93	C	1.57	a	1.22 - 2.00	C	5.02	b	4.34 - 5.81

Families are rank ordered at each experimental site. Values followed by the same letters are not significantly different within a site at the $\alpha = 0.05$ level (Tukey-Kramer test).
[1)] family identification - lob. represents loblolly pine with superior (sup.) and average (aver.) families and others identified by numbers, slash – slash pine family;
[2)] silvicultural treatment comparison – HI and C refer to high intensity and control treatments, respectively.

We found significant differences among the tested families in crown length, maximum crown diameter, and crown volume at all three experimental sites (all $P < 0.05$), even when variation in tree size was accounted for, using ANCOVA. The effect of silvicultural treatment was not statistically significant for crown length and crown diameter. Averaged across the sites and cultural treatments, the crowns of superior and average loblolly pine families were 31 and 21% longer, and 20 and 32% wider, respectively, than those of slash pine. Branch length adjusted to a common DBH and relative height within crowns differed between species ($P \leq 0.0018$), except at DeRidder ($P = 0.4849$), with slash pine having about 22% shorter branches than the two loblolly pine families (data not shown). However, the combination of differential distributions of branch lengths and branch angles within the crowns caused the superior loblolly pine

family to exhibit a wider middle crown compared to that of the slash and average loblolly pine families (Figure 2.2).

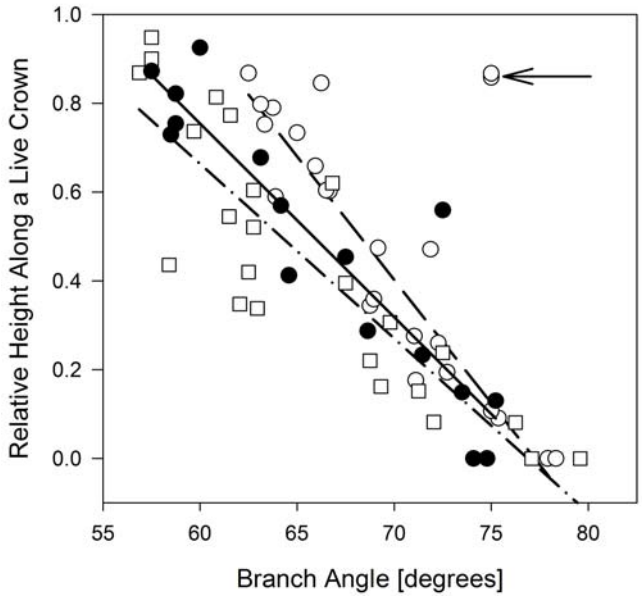

Figure 2.1. Distribution of branch angles along the length of the live crown for three examined families; --○-- average loblolly ($r^2 = 0.89$, $P < 0.0001$), –·–□–·– superior loblolly ($r^2 = 0.77$, $P < 0.0001$) and —●— slash pine ($r^2 = 0.84$, $P < 0.0001$). The arrow shows two outlier points that were excluded from analysis. Each point represents a mean value for a family in a cultural treatment at given height within the crown (node), calculated across sites (*n* for a particular node ranges from 1 to 12, depending upon the number of whorls among the 12 sample trees in each cultural treatment).

Slopes of the relationship between crown volume and DBH did not differ among families, but the intercept was significantly higher ($P < 0.0001$) for both loblolly pine families combined than for the slash pine family (Figure 2.3). Silvicultural treatment had no significant effect on crown volume. Thus, comparing trees across the experimental sites and cultural treatments, and accounting for the differences in tree size, the mean crown volume of slash pine constituted only about 45% of the mean values for both loblolly pine families (Figure 2.3).

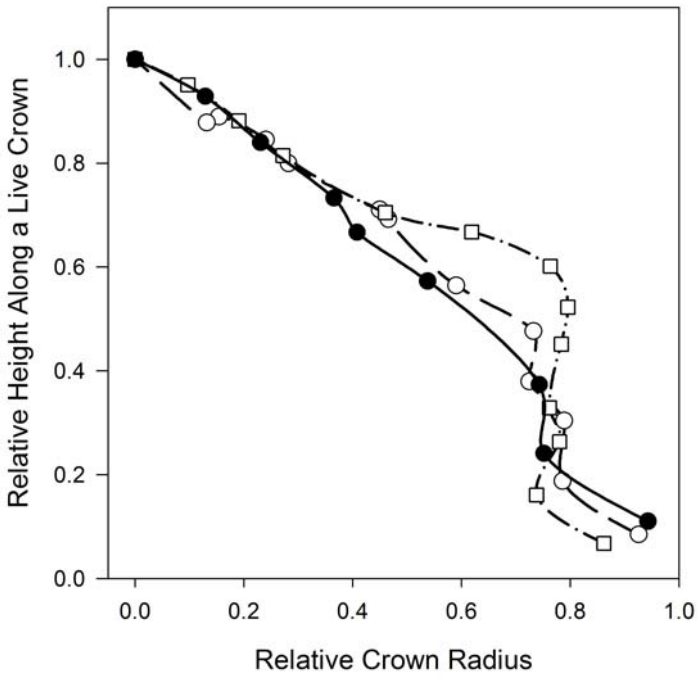

Figure 2.2. Distribution of relative crown radius (relative to maximum crown radius for a given family) along the length of the live crown for three examined families; --○-- average loblolly, –·–□–·– superior loblolly and —●— slash pine. For superior loblolly pine, the crown shape is not as conical as for the two other families. Each point represents a mean value for a family at given height within the crown, calculated across sites and cultural treatments (*n* for a particular point ranges from 2 to 24).

2.4.3. Leaf area and biomass

The three destructively sampled families differed in specific leaf area (SLA) at DeRidder ($P < 0.0001$) and Kirbyville ($P = 0.0011$), but not Bogalusa ($P = 0.8226$). On average, slash pine had lower SLA than both loblolly pine families (Table 2.3). A family × site interaction, although statistically significant ($P = 0.0059$), did not result in a change in family ranking in SLA among sites (Table 2.3). Significant differences in SLA between cultural treatments were present only at the Kirbyville site, where SLA was 7% lower in the HI than C treatment ($P = 0.0332$). The two pine species also differed in needle length. Slash pine had significantly longer needles (228.3 mm) than any loblolly

pine family in this experiment (157.2 and 160.6 mm for average and superior loblolly pine families, respectively (data not shown).

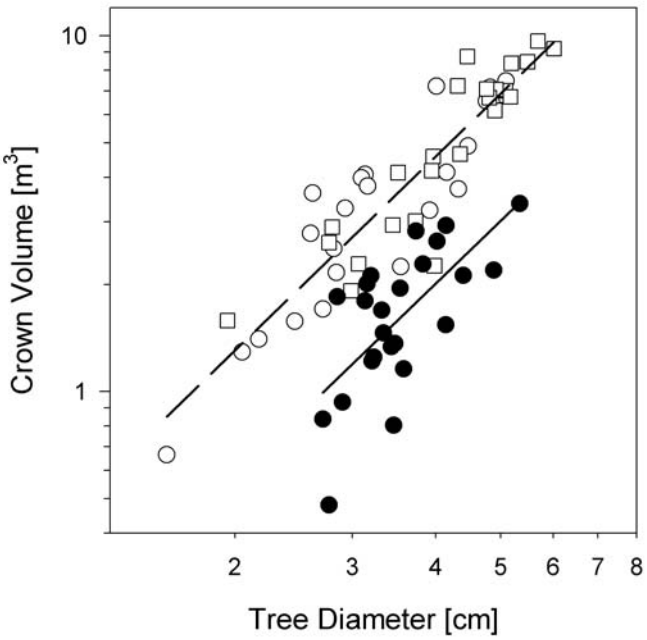

Figure 2.3. Relationship between tree diameter (DBH) and crown volume for three examined families; --○-- average loblolly, --□-- superior loblolly ($r^2 = 0.84$; $P < 0.0001$ for loblolly pine) and —●— slash pine ($r^2 = 0.45$; $P < 0.0001$). A single regression line was fit for two loblolly pine families combined as the slopes and intercepts did not differ between them. Regression fits are shown for individual trees of families across sites ($n = 24$ for each family).

Table 2.3. Average values and 95% confidence intervals of specific leaf area (SLA), aboveground leaf mass fraction (aLMF), aboveground leaf area ratio (aLAR) and leaf area density (LAD) for the examined families of loblolly and slash pine in two silvicultual treatments at three experimental sites in the West Gulf Coastal Plain area after 2 years of growth.

		SLA			aLMF			aLAR			LAD[1)]		
Site	**Family / culture**	**[$cm^2\ g^{-1}$]**		**95% C.I.**	**[$g_{leaf}\ g^{-1}_{aboveground}$]**		**95% C.I.**	**[$m^2_{leaf}\ kg^{-1}_{aboveground}$]**		**95% C.I.**	**[$m^2\ m^{-3}$]**		**95% C.I.**
Bogalusa	aver. lob.[2)]	121.4	a	114.6 - 128.3	0.35	b	0.32 - 0.37	4.20	b	3.73 - 4.66	4.24	b	3.31 - 5.43
	sup. lob.	127.5	a	120.7 - 134.4	0.41	a	0.39 - 0.43	5.25	a	4.80 - 5.70	5.01	b	3.95 - 6.37
	slash	120.5	a	112.5 - 128.4	0.43	a	0.40 - 0.45	5.17	a	4.69 - 5.65	9.33	a	7.22 - 12.04
	mean	**123.1**		**119.0 - 127.3**	**0.39**		**0.38 - 0.41**	**4.87**		**4.57 - 5.16**	**5.80**		**5.08 - 6.63**
	HI	123.2	a	116.8 - 129.6	0.43	a	0.40 - 0.45	5.28	a	4.82 - 5.75	7.40	a	5.78 - 9.48
	C	123.1	a	116.7 - 129.5	0.36	b	0.34 - 0.39	4.46	b	4.00 - 4.92	4.60	b	3.60 - 5.87
DeRidder	aver. lob.	129.7	b	122.8 - 136.5	0.36	b	0.32 - 0.40	4.67	b	4.12 - 5.23	4.64	b	3.72 - 5.78
	sup. lob.	148.3	a	141.4 - 155.1	0.45	a	0.41 - 0.48	6.59	a	6.03 - 7.15	7.44	a	5.97 - 9.27
	slash	114.6	c	107.7 - 121.5	0.47	a	0.44 - 0.51	5.43	b	4.87 - 5.99	10.85	a	8.70 - 13.53
	mean	**130.8**		**126.9 - 134.8**	**0.42**		**0.41 - 0.44**	**5.54**		**5.25 - 5.82**	**7.00**		**6.16 - 7.96**
	HI	133.3	a	128.5 - 138.1	0.43	a	0.40 - 0.46	5.70	a	5.25 - 6.16	7.60	a	6.35 - 9.09
	C	128.4	a	123.6 - 133.2	0.42	a	0.39 - 0.45	5.43	a	4.97 - 5.89	6.84	a	5.72 - 8.19
Kirbyville	aver. lob.	132.7	a	125.8 - 139.6	0.39	b	0.36 - 0.41	5.02	a	4.50 - 5.53	4.81	b	3.60 - 6.42
	sup. lob.	136.8	a	130.0 - 143.7	0.40	ab	0.38 - 0.43	5.64	a	5.09 - 6.19	4.86	b	3.57 - 6.61
	slash	116.0	b	109.1 - 122.8	0.45	a	0.42 - 0.47	5.17	a	4.71 - 5.63	9.80	a	7.56 - 12.70
	mean	**128.5**		**124.5 - 132.5**	**0.41**		**0.40 - 0.43**	**5.31**		**5.02 - 5.59**	**6.33**		**5.56 - 7.20**
	HI	123.9	b	118.0 - 129.9	0.41	a	0.39 - 0.43	5.11	a	4.73 - 5.50	6.09	a	4.90 - 7.55
	C	133.1	a	127.1 - 139.1	0.41	a	0.39 - 0.43	5.44	a	5.05 - 5.82	6.15	a	4.96 - 7.63
overall	**mean**	**127.5**			**0.41**			**5.24**			**6.78**		

Tree diameter was used as a covariate in the analysis of aLMF, aLAR, and LAD; therefore, least squares means adjusted for trees at a common size are shown. Values followed by the same letters are not significantly different within the experimental site (Tukey-Kramer test, $\alpha = 0.05$).

[1)] LAD mean values for families, cultural treatments and sites, and their confidence intervals were back-transformed from ln-transformed data.[2)] family and cultural treatments denoted as in Table 2.2.

To analyze the leaf area per tree, we calculated leaf area density (LAD) as the amount of foliage area per crown volume (m^2 leaf area m^{-3} crown volume), and tree diameter was used as a covariate in the analysis. Families differed significantly in terms of LAD at all experimental sites and slash pine had nearly doubled LAD compared to the loblolly pine families (Table 2.3). Thus, the slash pine family maintained a larger leaf area per given crown volume than the loblolly pine families (Figure 2.4). LAD was not influenced by the location of the experiment and the effect of cultural treatment was statistically significant only at Bogalusa ($P = 0.0266$), with the high intensity treatment increasing LAD by 61% compared to the control (Table 2.3).

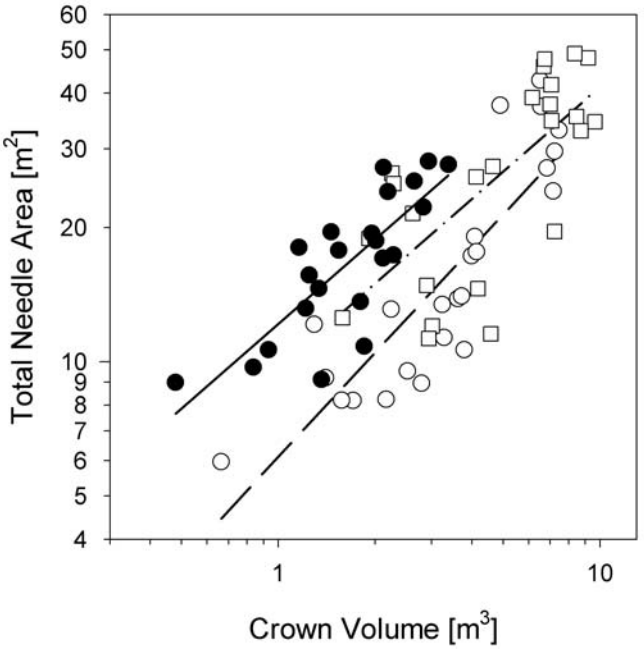

Figure 2.4. Relationship between crown volume and total needle area for three examined families; --○-- average loblolly ($r^2 = 0.75$; $P < 0.0001$), –·–□–·– superior loblolly ($r^2 = 0.50$; $P < 0.0001$) and —●— slash pine ($r^2 = 0.64$; $P < 0.0001$). Regression fits are shown for individual trees of families across sites ($n = 24$ for loblolly pine and 22 for slash pine families).

Aboveground leaf area ratio (aLAR), an important determinant of relative growth rate, is influenced both by SLA and the fraction of aboveground biomass partitioned into

leaves (aLMF), because LAR is a product of these two traits. Accounting for variation in tree size, the highest values of aLAR were recorded for the superior loblolly pine family, followed by those for slash pine (smaller by 10%) and the average loblolly pine family (smaller by 19%; Table 2.3). In contrast, aLMF of the slash pine family was greater by 18% than values for the average loblolly pine family ($P \leq 0.05$; Table 2.3), and greater by 7% than for the superior loblolly pine family across all experimental sites. There was a statistically significant family × site interaction term for aLAR ($P = 0.0255$), but families did not differ in their ranking among sites. The cultural treatment effect was significant only at Bogalusa, where aLAR and aLMF increased by 18 and 17%, respectively, in the HI compared to C treatment (Table 2.3).

The aLMF varied by 23% and SLA varied by 18% among families, which together contributed to a 23% range in aLAR among families (Table 2.3). Thus, the realized leaf area at the tree level seems to be modulated more by the relative amount of foliage than by differences in SLA in the examined families of loblolly and slash pine. However, SLA and aLMF influence aLAR independently, and at any given aLMF, trees with greater SLA will show higher aLAR and vice-versa.

2.4.4. Aboveground biomass partitioning

When the biomass of all aboveground components was analyzed in our stratified sample of trees adjusted to a common DBH in the analysis of covariance, branch biomass differed among families at all three locations (all $P \leq 0.0026$), but families did not differ for foliage biomass at any location or for bole biomass, except at the DeRidder site ($P = 0.0124$; Figure 2.5).

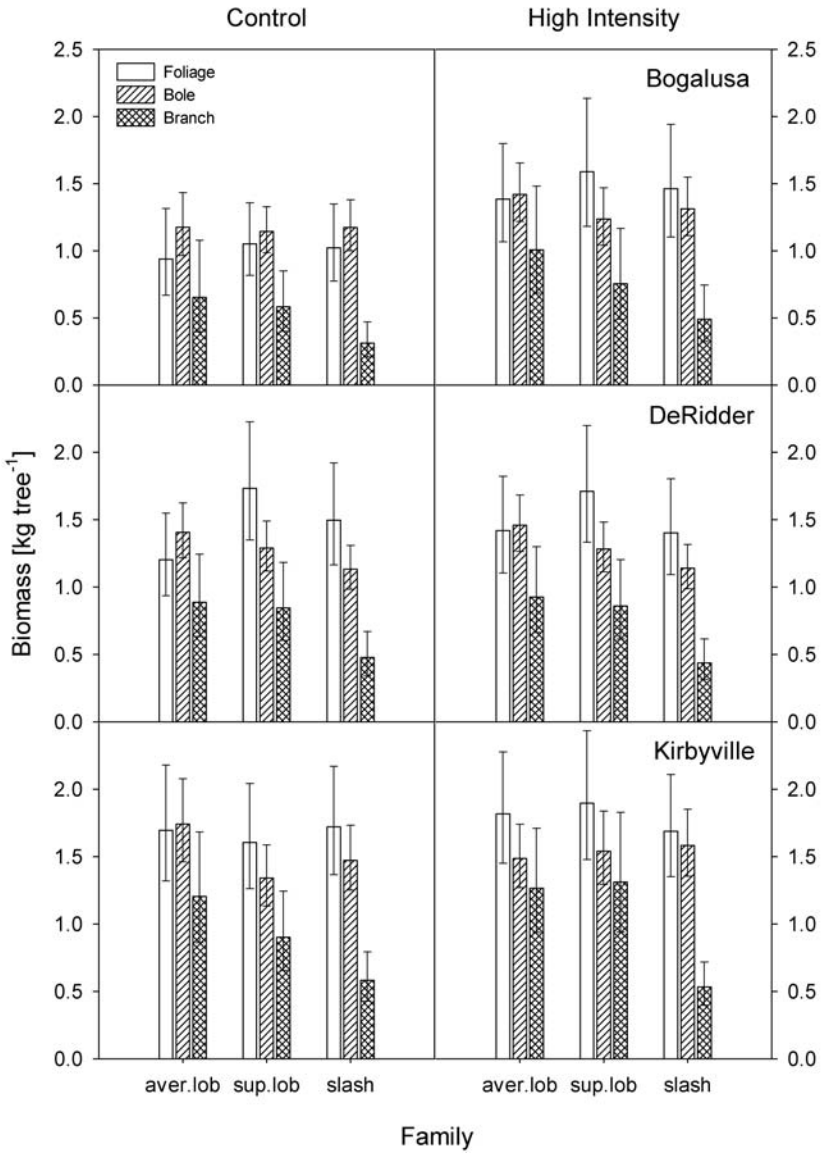

Figure 2.5. Values of least squares means of aboveground biomass components (kg) for each examined family adjusted to a common tree diameter (3.62 cm) in an analysis of covariance. Error bars show 95% confidence intervals. Family identification as in Table 2.2 (n = 4 for each family in each cultural treatment and site).

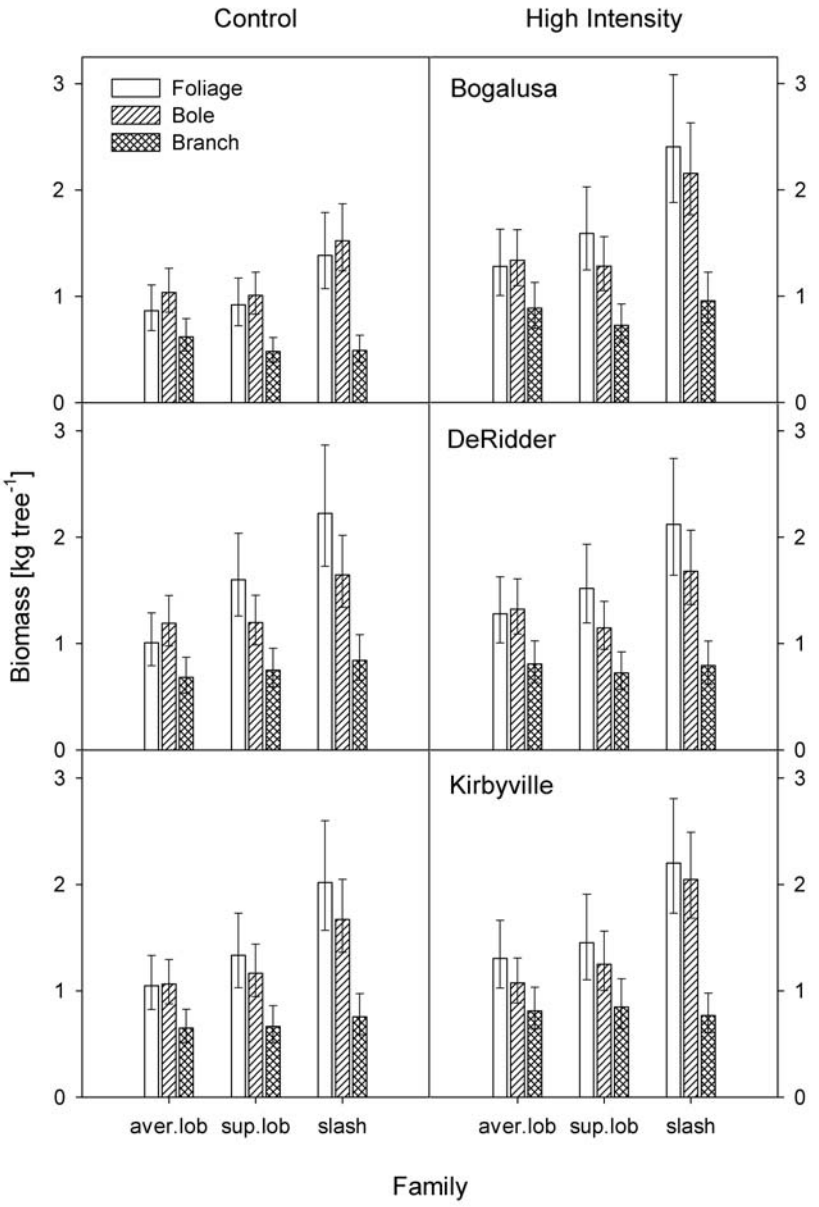

Figure 2.6. Values of least squares means of aboveground biomass components (kg) for each examined family adjusted to a common crown volume (2.91m^3) in an analysis of covariance. Error bars show 95% confidence intervals. Family identification as in Table 2.2 (n = 4 for each family in each cultural treatment and site).

Thus, we found significant differences in biomass partitioning patterns among the examined families (Figure 2.5). In general, slash pine had proportionally less aboveground biomass in branches (15%) than both loblolly pine families (23% for

superior loblolly and 26% for the average loblolly pine family, respectively). Although the superior loblolly pine family had the largest aboveground biomass overall, it partitioned the smallest proportion of its biomass into the bole (35%) among the three examined families (38% - average loblolly pine, and 40% - slash pine family). The relative partitioning of aboveground components was affected by cultural treatment only at the Bogalusa site, with a higher proportion of biomass in foliage and smaller proportion in the bole in the HI than C treatment (Figure 2.5).

2.4.5. Relationships of crown traits with biomass partitioning

In order to examine whether crown characteristics affected biomass allocation patterns among the tested families, we analyzed differences in biomass of all aboveground components with crown volume as a covariate. Differences in absolute accumulation of foliage and bole biomass were highly influenced by family at all sites (all $P \leq 0.0303$), whereas branch biomass did not differ significantly among families at any experimental site (Figure 2.6). The cultural treatment effect was significant only at the Bogalusa site for all aboveground biomass components ($P \leq 0.0006$), with trees in the HI treatment having greater biomass accumulation than in the C treatment (Figure 2.6). There were no family × treatment interaction effects for any biomass component at any location, implying similar responses to silvicultural treatment for all three families.

Slash pine trees, when compared at a similar crown volume as loblolly pine, produced more bole and needle biomass (Figure 2.6). However, the ratio of bole biomass to needle area per tree (a proxy for growth efficiency in these young stands) did not differ greatly among the three examined families. Growth efficiency defined as the slope of the relationship between bole biomass and total foliage area per tree was 0.76 for average loblolly pine, 0.71 for superior loblolly pine, and 0.72 for slash pine families. Therefore, any given change in leaf area per tree would lead to similar changes in bole-wood production in all three examined families (Figure 2.7).

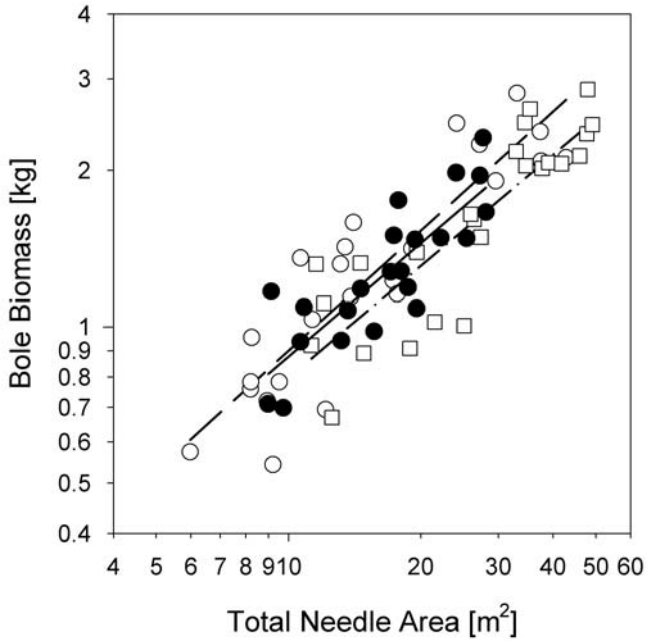

Figure 2.7. Relationship between bole mass and total needle area per tree (growth efficiency) for three examined families; --○-- average loblolly ($r^2 = 0.80$; $P < 0.0001$), –·–□–·– superior loblolly ($r^2 = 0.74$; $P < 0.0001$) and —●— slash pine ($r^2 = 0.71$; $P < 0.0001$). Regression fits are shown for individual trees of families across sites ($n = 24$ for loblolly pine and 22 for slash pine families).

2.5. Discussion

We found significant differences in productivity and crown characteristics among the examined families of loblolly and slash pine after the second year of growth at the experimental sites in the West Gulf Coastal Plain of Texas and Louisiana. In general, families differed in growth and loblolly pine tended to produce larger trees than slash pine except at the Bogulasa site. For most of the families in the experiment the interaction effect of genotype with site resulted from changes in the absolute differences among families at different sites rather than from changes in family rank. The average loblolly pine and slash pine families showed greater environmental sensitivity than other genotypes in the experiment. A persistent genotype × environment interaction would imply that these two genotypes might be suitable for planting only at certain type of sites

or climatic conditions. Slash pine is usually recommended over loblolly pine for planting on wet sites (Shoulders and Tiarks, 1980; Schultz, 1997). Our findings seem to corroborate these recommendations, because the Bogalusa site was wetter than the two other sites, based on the soil drainage class.

Earlier studies revealed that loblolly pine is usually more productive than slash pine in terms of aboveground biomass growth when compared in intensively managed plantations (Colbert et al., 1990; Jokela and Martin, 2000; Xiao et al., 2003a; Martin and Jokela, 2004b). Those differences, however, are likely to arise from greater responsiveness of loblolly than slash pine to intensive management (Colbert et al., 1990; Jokela and Martin, 2000; Roth et al., 2007), and might not necessarily exist without a high input of resources (Jokela and Martin, 2000). In the current study we have not confirmed a greater growth response of loblolly than slash pine to intensive silviculture. Fertilization and control of competing vegetation increased tree height and especially tree diameter compared to control treatment, but all families responded in a similar manner in terms of tree growth to intensive management through the first two years.

One of the objectives of our study was to test whether family differences in aboveground biomass productivity may be affected by crown size and structure. Slash pine trees in our experiment had significantly smaller crowns comprised of fewer and shorter branches than both loblolly pine families, even at a given tree size (see Figure 2.3). However, slash pine maintained a similar leaf area per tree as loblolly pine (see Figure 2.4), in effect, compensating for a reduced crown volume. Consequently, given a similar relationship of leaf area with biomass growth in both species, between-species differences in accumulated aboveground biomass were smaller than would have occurred in the absence of compensating adjustments in crown traits. Slash pine usually produces fewer bifurcations per branch than loblolly pine (Dalla-Tea and Jokela, 1991). Thus, in order to maintain similar leaf area to that of loblolly pine at a common tree size, slash pine with its smaller crowns must maintain more needles along the main stem and/or pack needles more densely on the branches. Slash pine needles were also significantly longer than for any loblolly pine family in this experiment, which may

largely account for the observed compensating pattern in leaf area display within crowns.

In our study, leaf area was a strong correlate of aboveground productivity in the young stands, highlighting the importance of leaf area in determining aboveground productivity in pine (Dalla-Tea and Jokela, 1991; Will et al., 2001; Borders et al., 2004; McGarvey et al., 2004). Differences in relative biomass allocation to leaves (aLMF), more so than in SLA, were responsible for variation in tree-level leaf area. Even though slash pine had much lower SLA than loblolly, its total leaf biomass was more than enough to offset this difference, leading to similar total leaf area and a greater leaf area density for slash pine trees than for loblolly pine across the examined range in tree size.

The superior loblolly pine family in our experiment had a different crown shape than two other families, with longer branches in the middle portion of the stem, which may have implications for light interception and growth. Crown structure and shape is likely to affect tree-level light interception by varying leaf area distribution or leaf angle within a crown, especially in young stands prior to canopy closure, where within-crown self-shading is more important than between-tree shading (Oker-Blom and Kellomaki, 1983). A positive relationship of aboveground biomass or wood volume accumulation with intercepted photosynthetically active radiation (PAR) is well documented in trees (Cannell, 1989; Dalla-Tea and Jokela, 1991; Wang et al., 1991; Will et al., 2001; 2005). Crown shape itself, however, seems to be less important for light interception than total leaf area and its distribution within the crowns, as was found in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stands (Wang and Jarvis, 1990b) and among trees of five families of loblolly pine (McCrady and Jokela, 1996). A uniform distribution of leaf area along a crown increases the vertical light gradient in a canopy, compared to a non-uniform distribution, leading to lower canopy-level photosynthesis (Wang et al., 1990). We were not able to quantify leaf area distribution in our study; however, if foliage distribution follows branch lengths within the crowns, our findings seem to confirm that non-uniform distribution of leaf area is more favorable for tree growth.

Other elements of crown structure together with crown shape contribute to effective light interception in the canopy. In the loblolly pine trees in our experiment, foliage area was displayed on a greater number of branches and longer branches than in slash pine, resulting in lower leaf area density and, most likely, reduced needle self-shading in such crowns. Similarly, Dalla-Tea and Jokela (1991) reported higher levels of PAR interception in canopies of loblolly pine than in slash pine, resulting from differences in leaf area index and crown structure. Total crown leaf area increased under high intensity treatment in our study compared to the control, although this effect was site-specific, but other crown traits were not affected by cultural treatment. This finding is similar to those of Vose (1988) and Gillespie et al. (1994), where N and P fertilization and thinning in loblolly pine stands increased leaf area accumulation, compared to controls, but did not change the vertical distribution of foliage.

The observed relationships of crown size and structure with tree growth were analyzed on the individual tree level in the absence of among-tree competition. While it is expected that canopy traits will change as the stand approaches canopy closure, early differences in canopy traits and tree growth at stand establishment may result in growth differences that persist through time. Thus, further studies are needed for more detailed clarification of the relationship of crown structure and crown shape with canopy light interception and tree growth throughout stand development.

2.6. Conclusions

We found differences in aboveground growth after the second growing period among seven families examined in our field study, with fertilization and control of competing vegetation improving tree growth compared to the control treatment. However, family rankings and the effectiveness of cultural treatment were site-dependent within the West Gulf Coastal Plain area in Texas and Louisiana.

Cultural treatment did not affect crown traits and biomass partitioning patterns, which were largely family or species-specific. Loblolly pine produced more flushes and

longer branches than slash pine. As a consequence, slash pine had significantly smaller crowns than loblolly pine trees of the same age or size. However, at a given crown size, slash pine maintained more leaf area and produced more bole-wood biomass than loblolly pine. Aboveground biomass growth was closely correlated with accumulated leaf area across a range of tree sizes. Although slash pine had lower SLA than loblolly pine, the relative allocation of biomass into foliage seemed to be more responsible for between-species differences in realized leaf area. The amount of bole-wood biomass produced per unit of leaf area (growth efficiency) was similar for both species and not affected by cultural treatment in the two-year old stands.

The superior loblolly pine family accumulated the greatest aboveground biomass among the three examined families, and had a different crown shape with longer branches in the mid-crowns. We suggest that leaf area distribution, associated with this crown shape and structure is responsible for more efficient crown-level light interception and CO_2 assimilation, leading to increased growth.

3. LEAF TRAITS IN RELATION TO CROWN DEVELOPMENT, LIGHT INTERCEPTION, AND GROWTH OF ELITE FAMILIES OF LOBLOLLY AND SLASH PINE*

3.1. Overview

Crown architecture and size influences leaf area distribution within tree crowns and has a large effect on light environment in forest canopies. The use of selected genotypes in connection with silvicultural treatments that tend to optimize site conditions in forest plantations provides both a challenge and an opportunity to study the biological and environmental determinants of forest growth. We investigated tree growth and crown development, along with leaf traits within crowns of two elite families of loblolly pine (*Pinus taeda* L.) and one slash pine (*Pinus elliottii* Mill.) at canopy closure. Two contrasting silvicultural treatments - repeated fertilization with control of competing vegetation (HI), and control (C), were applied at two experimental sites in the West Gulf Coastal Plain in Texas and Louisiana. At a common tree size (diameter at breast height), loblolly pine had longer and wider crowns and at the plot-level intercepted a greater fraction of PAR than slash pine. Leaf-level assimilation (A_{max}) rates and foliar N (both mass- and area-based) decreased, and specific leaf area (SLA) increased with increasing canopy depth. Observed leaf-trait gradients were steeper in crowns of loblolly pine than in slash pine for SLA and leaf N, but not A_{max}. The two pine species did not differ in leaf-level A_{max} and the effect of cultural treatment on A_{max} differed between sites. Leaf-level photosynthesis across all crown positions was correlated with leaf N, but the relationship differed between sites and treatments. Observed patterns of variation of leaf properties within crowns reflect acclimation to

* Reprinted with permission from "Leaf traits in relation to crown development, light interception, and growth of elite families of loblolly and slash pine" by Daniel J. Chmura and Mark G. Tjoelker, 2008, Tree Physiol., Copyright [2008] by Heron Publishing (accepted).

developing light gradients in stands with closing canopies. Tree growth was not directly related to the leaf-level rates of photosynthetic gas exchange, but there was a strong correlation between tree growth and plot-level light interception in both species, and growth efficiency not affected by silvicultural treatment. Leaf carbon assimilation, when coupled with leaf area and light interception at the crown and canopy level provide insight into family and silvicultural treatment differences in tree growth.

3.2. Introduction

Tree and forest growth are complex processes, which reflect the interactions of genetic and environmental factors influencing tree physiological and morphological properties for the acquisition and use of available resources - light, nutrients, water and CO_2. Plant productivity is inherently related to CO_2 exchange, but leaf-level photosynthetic rates are rarely correlated with plant growth (Poorter, 1989; Lambers et al., 1998; Poorter and Van der Werf, 1998). In forest canopies, scaling from leaf-level photosynthetic rates to the level of the whole stand is not straightforward, mainly because of the non-linearity of response of leaf photosynthesis to light, and heterogeneity of environmental conditions and leaf attributes within canopies (Medlyn et al., 2003). Big-leaf models of canopy assimilation usually give erroneous results as they fail to account for that variability (Boote and Loomis, 1991; Norman, 1993; Medlyn et al., 2003). The division of canopy leaf area into shaded and sunlit fractions provides improvements over the big-leaf modeling approach (Norman, 1993; De Pury and Farquhar, 1997). However, accounting for within-crown variability in leaf physiological and structural properties is a promising approach to improve estimations of canopy-level carbon gain (Norman, 1980; Norman, 1993). Thus, knowledge of canopy structure and leaf traits gradients within canopies is needed.

Photosynthetic carbon assimilation is highly dependent on light availability. A positive relationship of intercepted PAR (iPAR; photosynthetically active radiation 400 – 700 nm waveband) and biomass production is well documented in trees (Cannell,

1989; Dalla-Tea and Jokela, 1991; Wang et al., 1991; Will et al., 2001; Will et al., 2005). Total leaf area and its distribution within tree crowns have large effects on light interception in forest canopies (Wang and Jarvis, 1990b). Within tree crowns, leaf morphology and physiology is modulated in concert with changing light environments with canopy depth. In lower canopy levels, SLA (specific leaf area – leaf area per unit leaf biomass, $cm^2\ g^{-1}$) usually increases in comparison with the upper canopy (Ellsworth and Reich, 1993; Meir et al., 2002; McGarvey et al., 2004; Iio et al., 2005; Uemura et al., 2006). Area-based leaf nitrogen concentration (N_a, $g\ m^{-2}$) is usually higher in foliage from upper crown positions than at the bottom of a canopy (Ellsworth and Reich, 1993; McGarvey et al., 2004; Iio et al., 2005). In both broadleaved and coniferous species, leaves in the upper canopies were also found to have higher area-based photosynthetic rates at ambient light conditions (Tang et al., 1999; Gough et al., 2004b) and at light-saturated conditions (A_{max}) (Niinemets et al., 1998; Meir et al., 2002; Crous and Ellsworth, 2004; Iio et al., 2005) than in the lower crown positions. However, the photosynthetic capacity of leaves does not scale directly with growth-irradiance (Meir et al., 2002); therefore, leaf morphological adjustments in acclimation to low-light might be equally important as changes in biochemical properties (Niinemets et al., 1998; Meir et al., 2002) in influencing total canopy-level carbon gain.

Loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) are the main tree species planted throughout the Southeastern United States (McKeand et al., 2006). These species differ in aboveground biomass productivity and in growth response to intensive silvicultural treatments (Colbert et al., 1990; Jokela and Martin, 2000; Shiver, 2002; Martin and Jokela, 2004b; Roth et al., 2007) as well as crown architecture (Xiao et al., 2003a; Chmura et al., 2007; Emhart et al., 2007). Also genotypes within loblolly pine differ in growth and biomass accumulation (McCrady and Jokela, 1996; 1998; Roberts, 2002). However, leaf-level photosynthetic rates did not vary between loblolly and slash pine in a seedling study (Samuelson, 2000) or in four-year-old stands at various planting densities (Will et al., 2001). In contrast, McGarvey et al. (2004) found higher area-based photosynthetic rates for slash than for loblolly pine in stands

approaching canopy closure. Moreover, differences in leaf-level photosynthetic rates among genotypes within species and the relationships of photosynthesis with productivity are not well resolved, but together with crown structure these traits may be important determinants of growth differences.

Current silvicultural systems increasingly involve a deployment of genetically improved planting material, together with high-input silvicultural treatments to augment forest productivity (Allen et al., 2005; McKeand et al., 2006). As forest plantations become increasingly uniform (McKeand et al., 2003; McKeand et al., 2006), factors that limit tree growth should be identified in order to effectively alleviate those limitations. Fertilization, alone or applied in combination with control of competing vegetation, increased biomass production in many studies of loblolly and slash pine (Jokela et al., 2000; 2004; Martin and Jokela, 2004b). Leaf nitrogen concentration generally increases as a result of fertilization in pine stands (Teskey et al., 1994; Munger et al., 2003; Borders et al., 2004; Martin and Jokela, 2004a; Sword Sayer et al., 2004), although not always (Samuelson et al., 2001). However, the effects of intensive silvicultural treatments on leaf-level photosynthetic parameters are more variable. Net photosynthesis was higher in fertilized than in unfertilized stands (Teskey et al., 1994; Murthy et al., 1996; 1997) and in a seedling study (Samuelson, 2000), but non-significant or transient effects of fertilization (Munger et al., 2003; Gough et al., 2004a) or fertilization with irrigation (Samuelson et al., 2001) on leaf-level photosynthesis have been reported.

In this study we examined crown development and within-crown variability in leaf-level photosynthesis (A_a and A_m – area-based and mass-based net photosynthesis at light saturation A_{max}, respectively), leaf morphology and nitrogen in one slash pine and two loblolly pine families in their fourth and fifth growing seasons at canopy closure. The studied families were growing under two contrasting silvicultural treatments in the West Gulf Coastal Plain of Texas and Louisiana. Based on species and family differences in growth and crown size and shape reported from these stands at age 2 years (Chmura et al., 2007), we hypothesized that gradients of leaf morphology and physiology, related to acclimation to increased shading, would be steeper within crowns

of loblolly pine than slash pine. As the stand leaf area and biomass usually increases with fertilization in southern pines (Vose and Allen, 1988; Colbert et al., 1990; Will et al., 2002), we also expected the gradients to be more pronounced in the high intensity treatment than in the control treatment. The specific objectives of our study were to: i) compare family, species and silvicultural treatments, and their possible interactive effects on needle morphology and physiology during canopy closure; ii) analyze leaf N distribution within crowns at canopy closure, and whether the N-A_{max} relationship is influenced by expected changes in SLA within a canopy; and iii) correlate tree growth with leaf-level physiology in an attempt to resolve causes of growth differences among selected genotypes of the two southern pines.

3.3. Materials and Methods

3.3.1. Experimental sites

Two experimental sites located in the West Gulf Coastal Plain, in Kirbyville, Texas (30º 35' N, 93º 59' W) and in DeRidder, Louisiana (30º 51' N, 93º 21' W) constitute a part of the PPINES experiment (Pine Productivity Interactions on Experimental Sites), established by the Forest Biology Research Cooperative at the University of Florida. Long-term mean annual air temperatures are 19.2 and 19.3°C at Kirbyville (Town Bluff Dam weather station (NOAA, 2002a) and DeRidder (NOAA, 2002b), respectively. The annual long-term distribution of monthly rainfall is similar at both sites (Figure 3.1). The soil at the Kirbyville site is a moderately well drained fine-loamy, siliceous, semiactive, thermic Oxyaquic Paleudult of the Kirbyville series. At DeRidder the soil is a somewhat poorly drained fine-silty, siliceous, active, thermic Typic Glossaqualf of the Caddo series (http://websoilsurvey.nrcs.usda.gov).

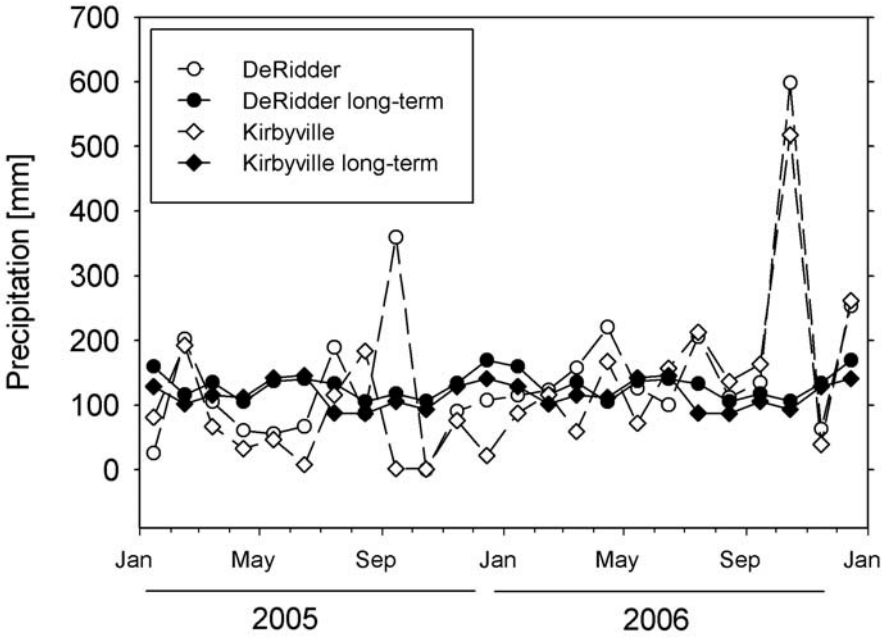

Figure 3.1. Monthly precipitation sums during the study period and long-term (1971-2000) means for the DeRidder and Kirbyville sites.

The experiment was established in a split-plot design in five randomized complete blocks at each site. The main-plot treatment consists of two contrasting silvicultural treatments: control (C) with fertilization (50.5 kg ha^{-1} N and 55.5 kg ha^{-1} P applied as 280.5 kg ha^{-1} of diammonium phosphate) and control of competing vegetation with Arsenal® (imazapyr) and Garlon™ (triclopyr) applied only at the time of site establishment, and high intensity (HI) with complete vegetation control and fertilization on a regular basis, beginning in the second growing season. The need for fertilizer additions was determined for each site based on yearly analyses of foliar nutrient concentrations based on critical foliage nutrient concentrations given in Gregoire and Fisher (2004) and the ability of the soil to supply nutrients. The cumulative elemental rates (kg ha^{-1}) applied though the fourth growing season reached 303 N, 123 P (as diammonium phosphate) and 66 K at DeRidder, and 255 N and 166 P (as diammonium

phosphate, urea and ammonium sulphate) at Kirbyville. Mg, Ca, S, B and Cu were applied only at DeRidder at 26.9, 32.5, 60.6, 0.4 and 3.4 kg ha^{-1}, respectively.

Five elite families of loblolly pine, one of slash pine, and one poorer-growing loblolly pine family were randomly assigned as sub-plots within cultural treatments. The experimental sites were established between November 2001 and January 2002. Containerized seedlings were planted in 2.4 × 3.3 m spacings (1,224 trees ha^{-1}) in 0.0588 ha pure-family plots (72 trees $plot^{-1}$). Details on site preparation and planting material are given in Chmura et al. (2007). Plots had not been thinned prior to this study. Survival in the blocks included in our analysis at the end of third growing season averaged 93% and 89% at the Kirbyville and DeRidder sites, respectively, and families or silvicultural treatments did not differ in survival.

For our study we sampled trees from three families, which were examined previously for allometric relationships and crown structure (Chmura et al., 2007). These are two families of loblolly pine, differing in growth and crown traits – Lob 1 (average growing) and Lob 5 (fast growing), and one slash pine family (Slash 6).

3.3.2. Measurements

Tree heights and diameters (DBH – diameter at 1.3 m), and crown traits were measured during the fourth growing season in the field, in March 2005, July 2005, and in February 2006, and at the end of the fifth growing season in December 2006. Crown traits included height to live crown, crown length, and crown diameter at the widest point in two directions (parallel and perpendicular to planting beds). Six trees per family plot were chosen to represent the range of tree sizes in each treatment combination; trees were sampled only from three blocks of the experiment at each site. In total, we sampled 108 trees (3 families / 2 cultural treatments / 6 trees / 3 blocks) at each site. Fewer trees were measured in February 2006 because of leaning trees and windthrow caused by hurricane “Rita” in September 2005, especially to slash pine. However, the recovery of leaning trees after the damage was satisfactory enough to allow sampling of nearly the

same number of trees in December 2006. Fourteen trees were substituted at Kirbyville and three at DeRidder, due to hurricane damage, but the numbers of sampled trees were the same in both years.

Plot-level PAR interception was measured with a 1-m long line quantum sensor (LI-191, LI-COR, Lincoln, NE, USA). Measurements were taken at 1 meter above the ground under the canopy on four (2005) and six (2006) transects within each plot, covering the whole inner-plot, with light conditions within and between tree rows equally represented. Below canopy measures were referenced against a cross-calibrated PAR sensor placed outside the stand in an open area. Measurements were taken during a four-hour sampling period centered on solar noon on clear, sunny days in October 2005 at both sites, and in September 2006 at DeRidder, and October 2006 at Kirbyville.

Needle morphology (projected specific leaf area – SLA, $cm^2\ g^{-1}$) and nitrogen concentrations were analyzed on foliage collected from three crown positions, representing the lower, middle and upper thirds of the live crown length. The distance between sampled crown positions depended on crown length, which ranged from 3.7 to 8.4 m among the loblolly pine families and from 3.1 to 6.5 m for slash pine. Thus, the distance between sampling points within crowns ranged from about 1 to 3 m. We collected needles of the last fully developed needle cohort (current-year flush) in July 2005 at Kirbyville and in September 2005 at DeRidder, approximately one month after fertilizer application at each site. Eighteen trees per family were sampled at each site for a total of 162 samples per site (3 families / 2 cultural treatments / 3 trees / 3 crown positions / 3 blocks). Needles were scanned on a flatbed scanner and projected needle area was determined on the digital images with WinRhizo software (Regent Instruments Inc., Canada). Samples were then oven-dried at 65 °C for at least 48 hours. Subsequently, needles were ground and analyzed for nitrogen (N) concentration with a NC analyzer (Flash EA1112, Thermo Electron Co., Milan, Italy). Leaf N was expressed both on leaf mass (N_m, $mg\ g^{-1}$) and area (N_a, $g\ m^{-2}$) basis.

In June 2006, we measured light-saturated rates of net photosynthesis to analyze variability of leaf-level photosynthetic CO_2 exchange (area-based A_a, $\mu mol\ m^{-2}\ s^{-1}$, and

mass-based A_m, μmol g^{-1} s^{-1}) within crowns of the selected families under contrasting cultural treatments. Branches were cut from three crown positions (lower, middle and upper) from the same aspect (west), immediately re-cut under water, and typically measured within 30 minutes. Measurements were conducted with the LI-COR 6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA), using the standard broadleaf chamber, on two needle fascicles (four to seven needles) attached to the branches. Conditions inside the chamber were set to the mean midday ambient air temperatures and relative humidities on the measurement dates and were: PAR 1600±0.9 (SD) μmol m^{-2} s^{-1} at both sites. Leaf-to-air vapor pressure deficit and relative humidity were 3.1± 0.2 kPa and 52.5±0.2% at DeRidder, and 3.5±0.4 kPa and 43.8±0.6% at Kirbyville. Reference CO_2 concentration was set at 380 μmol mol^{-1} and temperature at 32 °C at both sites. Our measurements at light saturation should well represent leaf photosynthetic capacity in southern pine stands, at least in well-lit crown positions. Measurements were completed over the course of two consecutive days at each site. Due to an instrument malfunction, 28 of 162 observations at the DeRidder site were excluded in the analysis. Needle sections enclosed in the leaf chamber were collected for SLA and leaf N determination. When possible, we sampled trees that were used in the crown-growth, SLA and leaf N study. Photosynthesis rates measured on current-year foliage were used in the analysis.

Leaf chlorophyll content was analyzed on the needles from the same needle cohort as measured for photosynthesis. Chlorophyll was extracted with 1 ml of dimethyl-sulfoxide (DMSO) from 20 mg of fresh needles cut into fine pieces (1-2 mm long). Absorbances were read at 649 and 665 nm with NanoDrop®ND-1000 spectrophotometer (NanoDrop Technologies, Inc. Wilmington, DE, USA). Concentrations of chlorophylls *a* and *b* were calculated using formulas provided by Wellburn (1994) for lower-resolution spectrophotometers and expressed on a leaf dry mass basis.

3.3.3. Analysis

Effects of family, cultural treatment, and family × treatment interaction on tree and crown growth were analyzed separately for the experimental sites and sampling periods. Because the measured trees were a stratified random sample that represented the range of tree sizes, crown traits were subjected to an analysis of covariance with tree volume index (dm^3, DBH^2×tree height) at the time of measurement as a covariate. Crown diameter was measured in two directions, but for the analysis, the two readings were averaged, as 90% of corresponding measurements had coefficients of variation less than 16% in all sampling periods. Stem biomass was estimated using allometric equations (Nemeth, 1973). Good agreement was found between parameters obtained from the loblolly and slash pine stands between four and 11 years of age (Nemeth, 1973), and our stands at age two years. At that time we did not observe family or site differences in the allometric relationship for stemwood mass (Chmura et al., 2007). Tree growth was defined as an annual increase in stem biomass. To test whether our sample trees were representative of the range of tree sizes we compared the plot level values with inventory data at age three years (relevant for the start of our analysis). The comparison revealed that trees in the smallest size classes might be underrepresented in our sample as the estimates of average tree size from stratified sample were slightly and consistently overestimated, compared to inventory data. However, the values of tree growth agreed very well with those based on the inventory data, therefore estimates of mean current annual biomass increment based on our sample trees are representative. An ANOVA was used to test for differences in tree growth with the block × cultural treatment interaction as the error term for the whole-plot effect (treatment; see also Table 3.1), and the residual error for sub-plot (family) and family × treatment interaction effects. Differences were regarded statistically significant at $P \leq 0.05$ and are hereafter referred to as such.

Gas exchange rates, needle morphology and foliage nitrogen data were analyzed on the individual tree level for each crown position in three blocks and two cultural

treatments, separately for the two experimental sites. Data were ln-transformed if needed to ensure the normality of distribution and uniformity of variance.

Family and cultural treatment means or least squares means were compared with the Tukey-Kramer HSD test at $\alpha = 0.05$. Contrast analysis was used to test for cultural treatment effects on the family means within sampling period and for species differences at each crown position. Linear regression analysis was used to examine relationships among traits. All analyses were completed with JMP 5.0.1 statistical software (SAS Institute Inc., Cary, NC, USA).

3.4. Results

3.4.1. Crown growth and light environment

The effect of cultural treatment on crown dimensions was generally small (differences smaller than 10%) and statistically significant only for crown length in March and July 2005 at DeRidder where crowns were longer on average by 7% in the C than HI treatment (data not shown). The examined families generally responded in a similar way to high intensity treatment within sites, as the family × cultural treatment interaction term was not significant, except in March 2005 for crown length at Kirbyville and crown diameter at DeRidder. Therefore, the data presented in Figure 3.2 were averaged across cultural treatments.

The observed dynamics of crown development (Figure 3.2) reflects expected changes in stands approaching canopy closure. The live crown receded from lower positions along the tree stem during the fourth and fifth growing seasons, and the largest change was observed at Kirbyville (Figure 3.2). At both sites, crown length and crown diameter increased significantly between March and July 2005 (Figure 3.2). Subsequently, both traits increased to the end of the next growing season (December 2006) for all three families at the DeRidder site. However, at the same time at Kirbyville, crown length decreased for the Lob 1 and Slash 6 families, in concert with increased heights to live crown, but remained the same in the Lob 5 family (Figure 3.2).

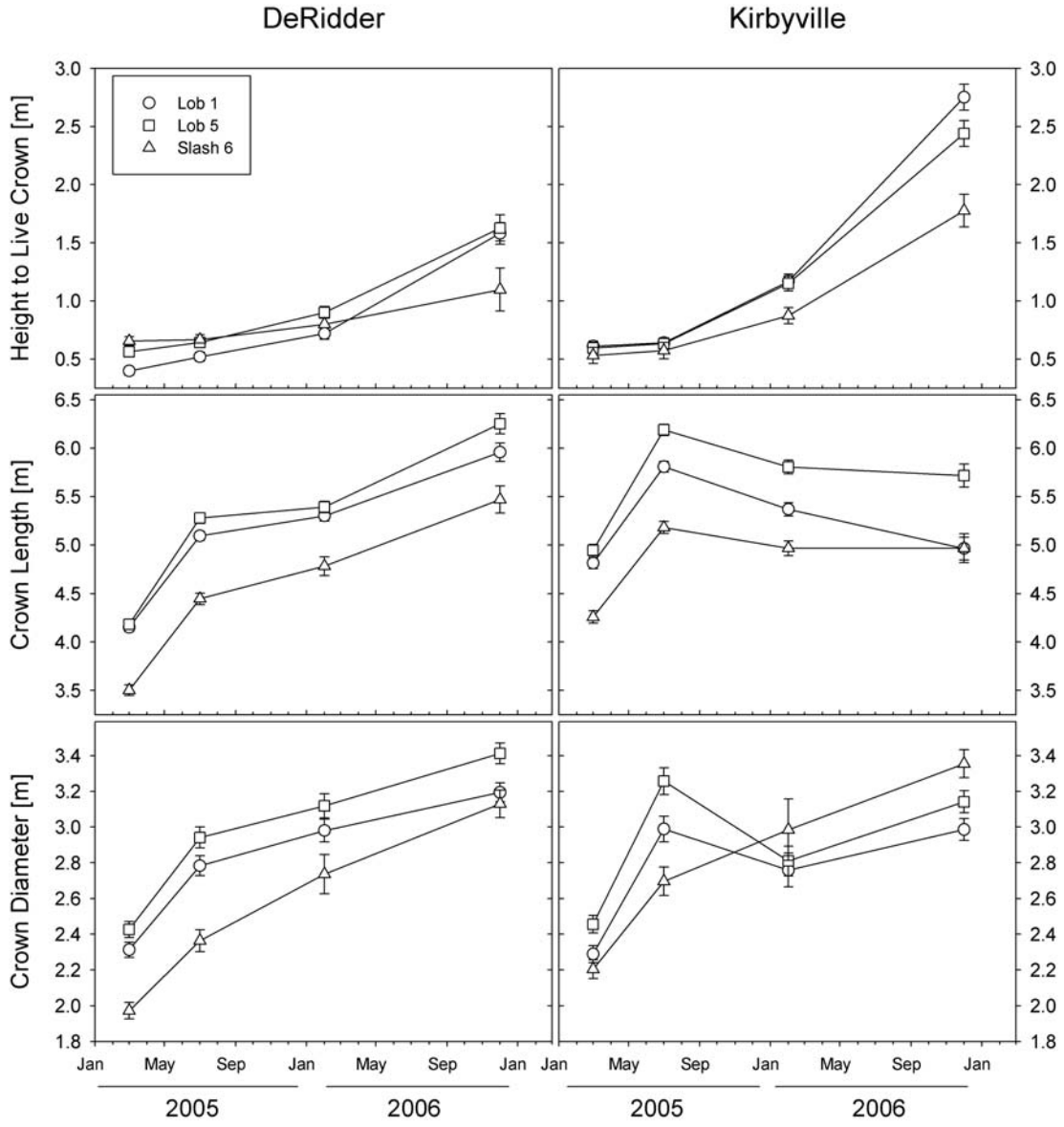

Figure 3.2. Crown development throughout the fourth (2005) and fifth (2006) growing seasons for the examined families of loblolly and slash pine at two experimental sites in the West Gulf Coastal Plain area. Values of height to live crown, crown length and crown diameter are least squares means adjusted to a common tree size ($DBH^2 \times Ht$, volume index) in an analysis of covariance across two cultural treatments. Error bars show standard errors of the mean; n ranges from 8 to 36 for each point.

Crown diameter at Kirbyville increased between July 2005 and December 2006 for slash pine, but for loblolly pine families it recovered to the values observed in July 2005 after a decrease in February (Figure 3.2). Thus, at the Kirbyville site at the end of fifth growing season, slash pine crowns were wider than those of loblolly pine when variation in tree size was accounted for. However, at both sites loblolly pine families in general had longer and wider crowns than the slash pine family (Figure 3.2).

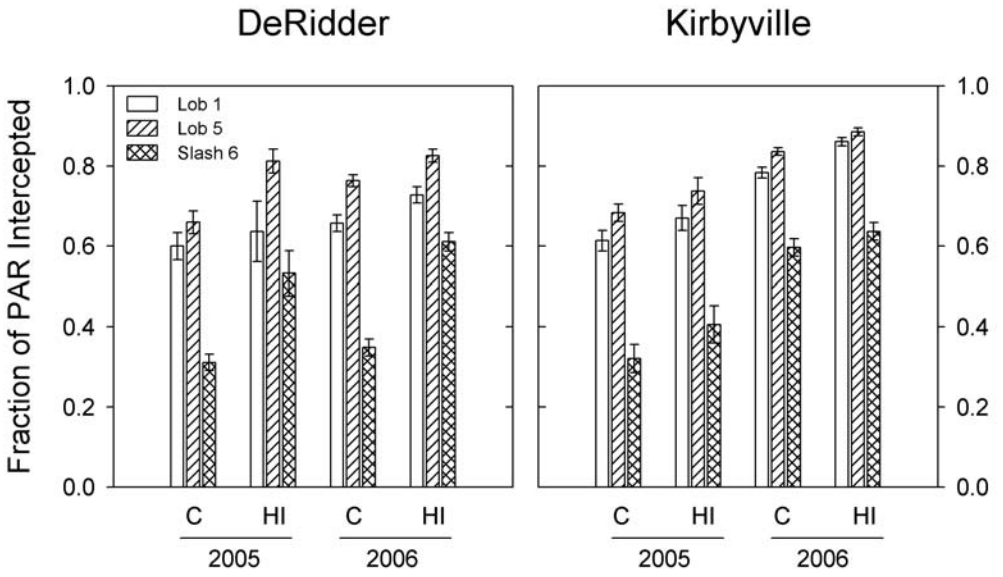

Figure 3.3. Mean (s.e., n = 3 plots) proportion of intercepted photosynthetically active radiation (PAR) at the plot level for examined families of loblolly and slash pine in the fourth (2005) and fifth (2006) growing seasons at two sites in the West Gulf Coastal Plain area in two contrasting cultural treatments – control (C) and high intensity (HI).

The range of plot-level PAR interception was similar at both experimental sites, and species differences were significant in both growing seasons, with loblolly pine families intercepting more light than the slash pine family (Figure 3.3). We have not observed significant effects of cultural treatment on plot-level light interception, except for a family×treatment interaction at DeRidder in 2006. At that site, PAR interception was 75% higher under HI treatment than in the C treatment for slash pine, whereas the

difference between treatments for loblolly pine was less than 10% in most cases (Figure 3.3). All three families intercepted more PAR in 2006 than in the 2005 growing season, although the difference was not statistically significant at DeRidder (Figure 3.3).

3.4.2. Tree growth

During the fourth and fifth growing seasons, tree height and diameter differed between the two pine species in all sampling periods on the stratified sample of trees (data not shown). Family and cultural treatment effects on the current stem biomass increment were significant in both seasons at both locations, except for the cultural treatment effect in 2005 at DeRidder (Table 3.1). The Lob 5 family had 42 to 75% greater stemwood growth than the Slash 6 family, and the Lob 1 family had intermediate stem increments (Table 3.1). Tree growth rates in the fourth growing season were only 52 to 69% as high as those in the next year, with somewhat smaller differences at Kirbyville than at DeRidder (Table 3.1). Tree growth in the HI treatment was 30-41% greater than in the C treatment (Table 3.1). Family and cultural treatment effects were independent as there was no significant family × treatment interaction.

3.4.3. Leaf morphology and chemistry gradients within crowns

Specific leaf area (SLA) varied with crown position in both years at both experimental sites, and was not influenced by cultural treatment (Figure 3.4, Table 3.2). The family effect was significant, with the Lob 5 family having the highest SLA at all crown positions and the Slash 6 family having the lowest SLA at both sites in both years (Figure 3.4). As expected, SLA increased from the upper to the lower crown, except for the slash pine family in 2005. The increase in SLA with increasing crown depth was much greater in loblolly pine (10-30%) than in slash pine (4-15%), resulting in a significant family × crown position interaction effect at both sites (Figure 3.4, Table 3.2). Although the family × treatment interaction term was statistically significant for

SLA at DeRidder in 2006 (Table 3.2), the family ranks remained unchanged across sites and cultural treatments.

Table 3.1. Least squares means values (95% C.I.) of stemwood biomass increments in the fourth (2005) and fifth (2006) growing seasons for the examined families of loblolly and slash pine growing in two contrasting cultural treatments at two sites in the West Gulf Coastal Plain area. ANOVA results are given at the bottom of the table. Family means assigned with the same superscript letters are not significantly different within a site and measurement period (Tukey-Kramer test, $\alpha = 0.05$).

			DeRidder			
			Stemwood Biomass Increment [kg year^{-1}]			
Family	**Treatment**		**2005**		**2006**	
Lob 1	C[1)]		3.32[2)]	(2.90 - 3.82)	6.35	(5.65 - 7.13)
	HI		4.47	(3.90 - 5.13)	7.31	(6.51 - 8.22)
		mean	**3.86^{b}**	**(3.50 - 4.25)**	**6.81^{a}**	**(6.28 - 7.40)**
Lob 5	C		4.01	(3.50 - 4.61)	7.09	(6.31 - 7.97)
	HI		5.25	(4.56 - 6.05)	9.38	(8.31 - 10.57)
		mean	**4.59^{a}**	**(4.16 - 5.07)**	**8.15^{a}**	**(7.50 - 8.87)**
Slash 6	C		2.33	(1.98 - 2.74)	4.05	(3.53 - 4.65)
	HI		3.17	(2.76 - 3.64)	5.87	(5.22 - 6.59)
		mean	**2.72^{c}**	**(2.44 - 3.02)**	**4.88^{a}**	**(4.46 - 5.33)**
			Kirbyville			
Family	**Treatment**		**2005**		**2006**	
Lob 1	C		3.04	(2.63 - 3.50)	5.74	(4.77 - 6.90)
	HI		5.13	(4.45 - 5.91)	8.40	(6.98 - 10.10)
		mean	**3.95^{b}**	**(3.57 - 4.36)**	**6.94^{a}**	**(6.09 - 7.91)**
Lob 5	C		4.13	(3.60 - 4.74)	6.26	(5.23 - 7.49)
	HI		5.84	(5.07 - 6.73)	9.48	(7.88 - 11.40)
		mean	**4.91^{a}**	**(4.45 - 5.42)**	**7.70^{a}**	**(6.77 - 8.76)**
Slash 6	C		2.91	(2.42 - 3.50)	4.25	(3.34 - 5.41)
	HI		3.39	(2.85 - 4.02)	5.40	(4.31 - 6.75)
		mean	**3.14^{c}**	**(2.77 - 3.56)**	**4.79^{b}**	**(4.06 - 5.65)**

Source of Variation	**d.f.**	***P* > F**		***P* > F**	
		DeRidder	**Kirbyville**	**DeRidder**	**Kirbyville**
treatment[3)]	1	0.0638	**0.0116**	**0.0198**	**0.0295**
family	2	**<0.0001**	**<0.0001**	**<0.0001**	**0.0001**
family × treatment	2	0.9646	0.0754	0.1716	0.6900

[1)] C – control treatment, HI – high intensity treatment, [2)]Least squares means and confidence intervals were back-transformed from ln-transformed data. [3)]The block × treatment interaction term with 2 d.f. was used as the error term for the block and treatment effects.

Table 3.2. Analysis of variance P > F values for area-based (N_a, g m^{-2}) and mass-based (N_m, mg g^{-1}) leaf nitrogen, specific leaf area (SLA, cm^2 g^{-1}), concentrations of chlorophyll (Chl, µmol g^{-1}), area-based (A_a, µmol m^{-2} s^{-1}) and mass-based (A_m, µmol g^{-1} s^{-1}) photosynthesis, and instantaneous photosynthetic nitrogen-use efficiency (iPNUE, µmol $molN^{-1}$ s^{-1}) in needles of examined families of loblolly and slash pine growing in two contrasting cultural treatments at two sites in the West Gulf Coastal Plain area.

					DeRidder						
		2005			2006						
Source of Variation	**d.f.**	**N_a**	**N_m**	**SLA**	**N_a**	**N_m**	**SLA**	**Chl**	**A_a**	**A_m**	**iPNUE**
block[1)]	2	0.4310	0.3218	0.3814	0.6955	0.8399	0.4552	0.0895	**0.0075**	**0.0051**	**0.0041**
treatment	1	0.7572	0.2496	0.1835	0.7725	0.8226	0.9330	0.2831	0.0877	0.4328	0.2473
family	2	**0.0010**	**<0.0001**	**<0.0001**	**0.0455**	**<0.0001**	**<0.0001**	**<0.0001**	0.8037	0.0708	0.9836
family × treatment	2	**0.0183**	**0.0175**	0.1313	0.0786	0.1991	**0.0126**	0.2779	0.8896	0.6746	0.5270
crown position	2	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.5453	**<0.0001**	**0.0001**	0.0565
family × cr. pos.	4	**<0.0001**	**0.0005**	**0.0068**	**0.0001**	**0.0041**	**<0.0001**	0.6483	0.6901	0.7639	0.7830
treatment × cr. pos.	2	0.2325	0.3134	0.6698	0.7571	0.9212	0.6707	0.2958	0.0981	0.0849	0.1118
error d.f.		143	143	144	134	134	134	130	110	110	110
					Kirbyville						
		2005			2006						
Source of Variation	**d.f.**	**N_a**	**N_m**	**SLA**	**N_a**	**N_m**	**SLA**	**Chl**	**A_a**	**A_m**	**iPNUE**
block	2	0.2954	0.6813	0.0814	0.7480	0.6847	0.3335	**0.0210**	0.4497	0.4955	0.4486
treatment	1	**0.0255**	**0.0340**	0.1997	0.3313	0.1269	0.5953	**0.0020**	0.0805	0.1053	0.0834
family	2	0.1491	**<0.0001**	**<0.0001**	0.0930	**<0.0001**	**<0.0001**	**<0.0001**	**0.0006**	**0.0002**	**0.0007**
family × treatment	2	**0.0342**	**<0.0001**	0.9982	0.3252	0.1526	0.0676	0.1637	**0.0284**	0.0908	**0.0086**
crown position	2	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0085**	**0.0655**	0.6961	0.0652
family × cr. pos.	4	**0.0052**	**0.0093**	**0.0011**	**0.0011**	**0.0051**	**0.0026**	0.0673	0.2633	0.4579	0.5596
treatment × cr. pos.	2	0.8114	0.7143	0.1467	0.9725	0.7928	0.7887	0.8880	0.9096	0.7650	0.4550
error d.f.		141	141	143	126	126	128	128	128	128	126

[1)] The block × treatment interaction term with 2 d.f. was used as the error term for the block and treatment effects.

Overall, families differed in mass-based (N_m) and area-based (N_a) leaf N (Table 3.2). This variation was largely the result of species differences; slash pine had lower leaf N_m than the two loblolly pine families at all crown positions (Figure 3.4). Leaf N concentrations decreased with increasing canopy depth from the upper to the lower canopy in loblolly pine families in 2005, and in both pine species in 2006. Species differences in N_a were less pronounced than for N_m, due to species differences in SLA (Figure 3.4). The nitrogen gradient with canopy depth was steeper in crowns of loblolly pine than in slash pine, which was reflected in a significant family × crown position interaction term at both sites and years (Table 3.2).

In 2005, a significant family × treatment interaction term for foliar N (Table 3.2) resulted from a change of family rankings in N_a across treatments at both sites. At DeRidder, N_a was reduced in the HI compared to the C treatment by 5% in slash pine, in contrast to both loblolly pine families (1-10% increase), and at Kirbyville, the Lob 1 family was more responsive (34% increase in N_a) to HI treatment than the two other families (Lob 5 and Slash 6, 22 and 14% increase, respectively). Similar patterns were found for N_m as for N_a, resulting in comparable trends in foliar nitrogen within crowns and between species. Neither cultural treatment nor interaction effects involving treatment were statistically significant in the next growing season.

Concentrations of chlorophyll *a* and *b* differed among examined families at both sites (Table 3.2), with loblolly pine families having on average 12-38% higher chlorophyll concentrations than slash pine (Table 3.3). The effect of crown position was significant for that trait only at the Kirbyville site (Table 3.2), where leaf chlorophyll concentrations were 7 and 11% greater at the lower and middle crown positions, respectively, than in the upper canopy. In addition, chlorophyll concentration was increased by 19% under HI treatment compared to control at Kirbyville, but not at DeRidder (Table 3.2 and 3.3).

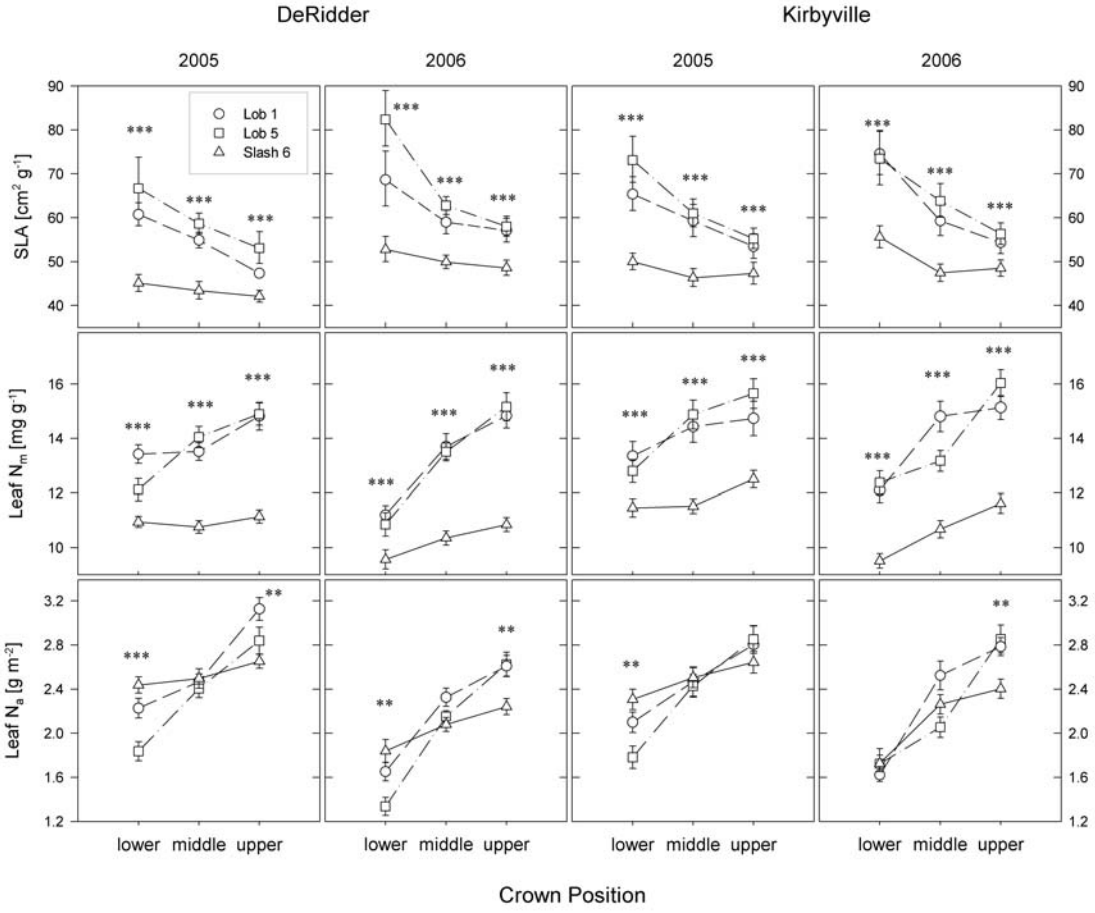

Figure 3.4. Within-crown variability of SLA, mass-based (N_m) and area-based (N_a) leaf nitrogen for examined families of loblolly and slash pine at two experimental sites in the West Gulf Coastal Plain area. Each point represents a mean calculated across two cultural treatments (n = 18). Error bars show 95% confidence intervals for SLA and standard error of the mean for N. Asterisks indicate the significance level for the contrast analysis between two species at each crown position $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$.

3.4.4. Leaf-level photosynthesis and iPNUE

Light-saturated rates of leaf-level photosynthesis, when measured midseason in June, differed among tested families at Kirbyville expressed both on leaf area (A_a) and leaf mass basis (A_m, Table 3.2, Figure 3.5). However, species differences were not statistically significant, except for A_m of the upper crowns (Figure 3.5). At the Kirbyville site, the Lob 5 family had significantly lower A_a than two other families at lower and

middle crown positions, and a lower A_m than the Lob 1 family (Figure 3.5). The cultural treatment effect on net CO_2 assimilation rate was not statistically significant at DeRidder, and was dependent upon family at Kirbyville (family × treatment interaction, Table 3.2). The reduction in A_a under the HI treatment compared to C at Kirbyville was significantly greater for the slash pine family (55%) than for the Lob 1 and Lob 5 families (42 and 30% decrease, respectively).

Table 3.3. Mean values (s.e.) of instantaneous photosynthetic nitrogen-use efficiency (iPNUE) and leaf total chlorophyll concentrations measured within crowns of examined families of loblolly and slash pine at two sites in the West Gulf Coastal Plain area. Means followed with the same superscript letters are not significantly different among crown positions in each family and cultural treatment.

		DeRidder							
Family	**Crown Position**	**iPNUE [μmol molN^{-1} s^{-1}]**				**Chlorophyll [μmol g^{-1}]**			
		Control		**High Intensity**		**Control**		**High Intensity**	
Lob 1	lower	70.28^{a}	(17.60)	26.69^{b}	(11.73)	0.31^{a}	(0.02)	0.38^{a}	(0.04)
	middle	53.48^{a}	(13.23)	65.58^{ab}	(11.12)	0.35^{a}	(0.03)	0.31^{a}	(0.03)
	upper	68.97^{a}	(10.61)	75.58^{a}	(10.60)	0.31^{a}	(0.02)	0.30^{a}	(0.02)
Lob 5	lower	53.75^{a}	(23.67)	61.14^{a}	(24.64)	0.35^{a}	(0.03)	0.35^{a}	(0.05)
	middle	50.96^{a}	(13.11)	65.68^{a}	(16.45)	0.35^{a}	(0.03)	0.33^{a}	(0.02)
	upper	62.73^{a}	(7.70)	74.73^{a}	(15.34)	0.35^{a}	(0.02)	0.36^{a}	(0.03)
Slash 6	lower	49.15^{a}	(16.44)	41.78^{a}	(13.50)	0.29^{a}	(0.02)	0.26^{a}	(0.02)
	middle	61.85^{a}	(14.10)	76.83^{a}	(13.06)	0.28^{a}	(0.02)	0.24^{a}	(0.01)
	upper	62.05^{a}	(12.54)	74.29^{a}	(10.39)	0.29^{a}	(0.02)	0.25^{a}	(0.02)
		Kirbyville							
		Control		**High Intensity**		**Control**		**High Intensity**	
Lob 1	lower	96.68^{a}	(21.51)	67.71^{a}	(11.99)	0.35^{a}	(0.04)	0.46^{a}	(0.04)
	middle	86.70^{a}	(11.90)	40.19^{a}	(7.29)	0.37^{a}	(0.03)	0.45^{a}	(0.02)
	upper	76.27^{a}	(9.69)	49.77^{a}	(8.65)	0.31^{a}	(0.02)	0.38^{a}	(0.02)
Lob 5	lower	54.40^{a}	(36.81)	39.81^{a}	(9.17)	0.36^{a}	(0.03)	0.40^{a}	(0.02)
	middle	53.40^{a}	(13.35)	33.96^{a}	(11.76)	0.36^{a}	(0.02)	0.46^{a}	(0.03)
	upper	57.88^{a}	(11.19)	40.40^{a}	(8.68)	0.35^{a}	(0.02)	0.41^{a}	(0.03)
Slash 6	lower	127.84^{a}	(12.23)	39.08^{a}	(13.13)	0.30^{a}	(0.02)	0.34^{a}	(0.02)
	middle	87.71^{b}	(9.13)	47.61^{a}	(10.10)	0.30^{a}	(0.01)	0.32^{a}	(0.01)
	upper	81.72^{b}	(10.27)	33.37^{a}	(6.95)	0.27^{a}	(0.01)	0.33^{a}	(0.01)

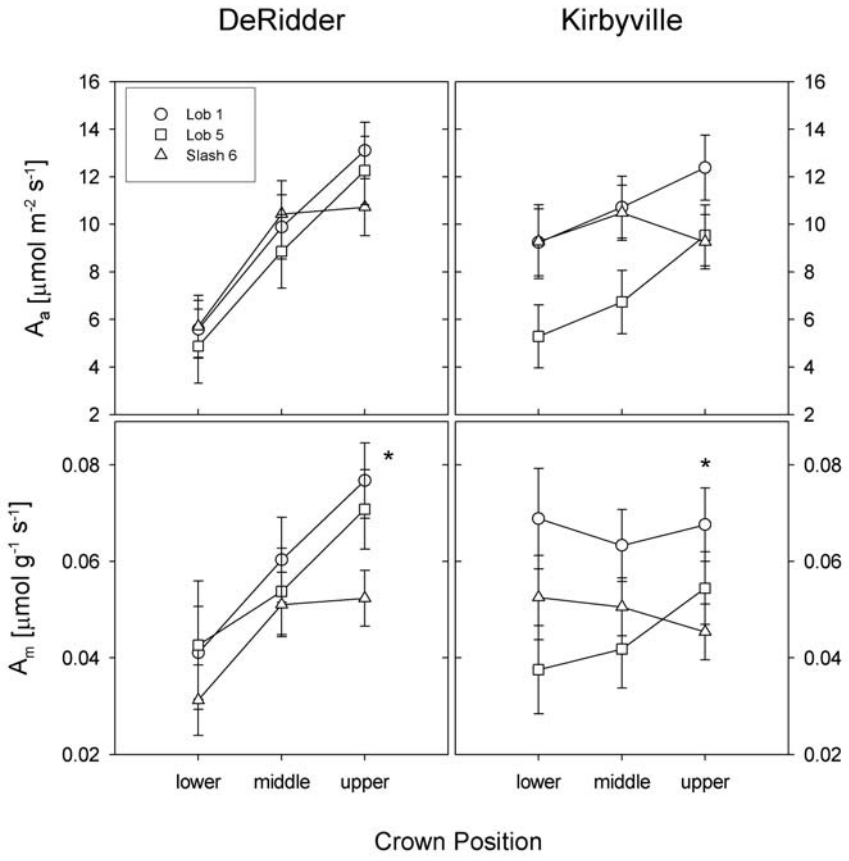

Figure 3.5. Leaf-level area-based (A_a) and mass-based (A_m) light-saturated photosynthesis rates within crowns of the examined families of loblolly and slash pine at two experimental sites in the West Gulf Coastal Plain area. Values were averaged across two cultural treatments (n ranges from 14 to 18 for each point). Error bars show the standard error of the mean. Asterisks indicate the $P \leq 0.05$ significance level for the contrast analysis between two species at a given crown position.

The effect of crown position on leaf-level photosynthesis was significant at DeRidder, but not at Kirbyville, although similar patterns were evident at both sites for A_a (Table 3.2, Figure 3.5). At the DeRidder site, we found an increase in A_a from the lower to the middle crown positions in all tested families, and in A_m in the Lob 1 family (Figure 3.5).

Families differed in instantaneous photosynthetic nitrogen-use efficiency (iPNUE) at Kirbyville (Table 3.2), with the Lob 5 family having the lowest iPNUE (Table 3.3). However, the family × cultural treatment interaction was statistically

significant at that site (Table 3.2). Although, the iPNUE was reduced in the HI treatment compared with control for all three families, the effect was much stronger for the slash pine family with an overall 90% decrease than for the two loblolly pine families (31-39% reduction, Table 3.3). At DeRidder, the effect of cultural treatment on iPNUE was not statistically significant (Table 3.2). The change in the iPNUE among crown positions was not statistically significant, except for the Lob 1 family in the HI treatment at DeRidder and Slash 6 family under the C treatment at Kirbyville (Table 3.3).

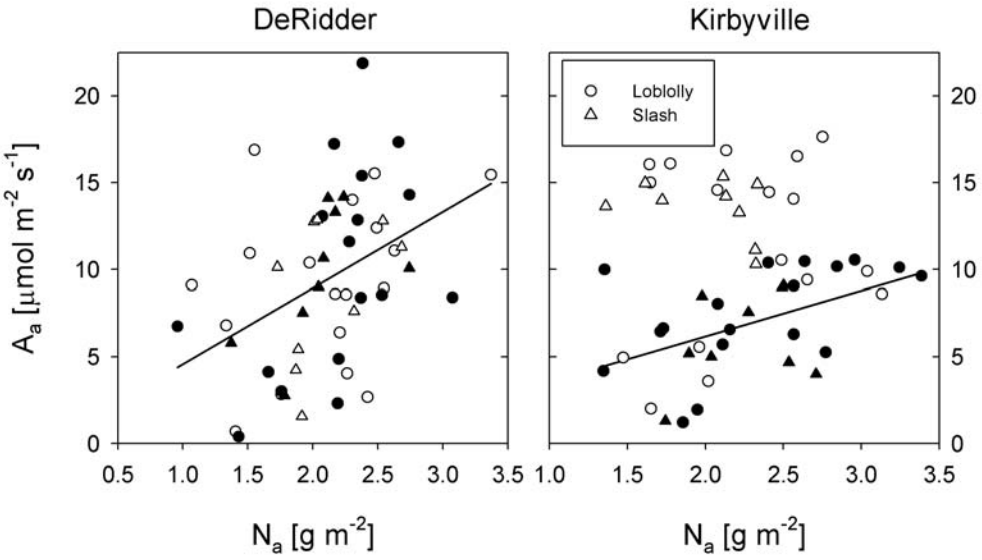

Figure 3.6. Relationship between area-based photosynthesis and leaf nitrogen for examined families of loblolly and slash pine at two experimental sites in the West Gulf Coastal Plain area. Open symbols represent the control treatment and closed symbols represent the high intensity treatment. Each point represents plot-level mean at each crown position (n = 3). Lines show regressions fits to all data at DeRidder ($r^2 = 0.18$, $P = 0.0015$, n = 53) and high intensity treatment at Kirbyville ($r^2 = 0.23$, $P = 0.0118$, n = 27).

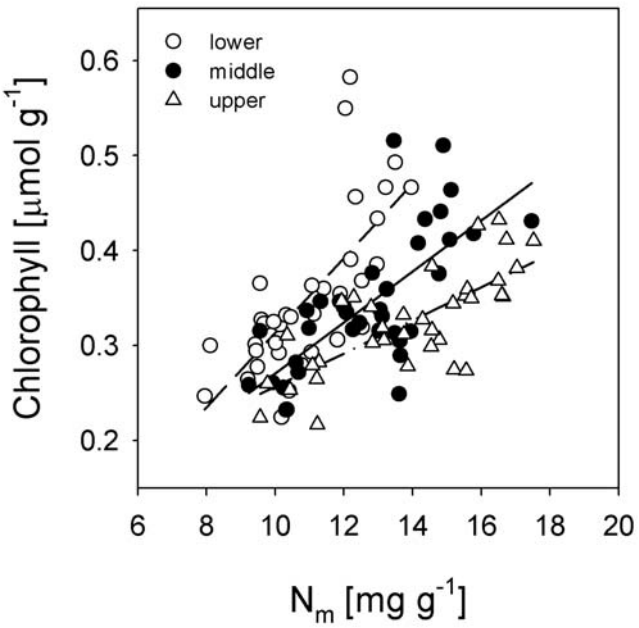

Figure 3.7. Relationship between total chlorophyll and leaf nitrogen concentrations in crowns of examined families of loblolly and slash pine. Regressions were fit for crown positions across taxa and experimental sites (n = 36 at each crown position). $Y = -0.079 + 0.039X$, $r^2 = 0.51$, n = 35 for lower crown; $Y = 0.0019 + 0.027X$, $r^2 = 0.51$, n = 36 for middle crown, and $Y = 0.082 + 0.017X$, $r^2 = 0.55$, n = 36 for upper crown positions; all $P < 0.0001$.

3.4.5. Trait relationships

Area-based photosynthesis rate was positively correlated with leaf N across all treatment combinations at DeRidder, but only for the high intensity treatment at Kirbyville (Figure 3.6). Similar relationships were found when both photosynthesis and leaf N were expressed on the leaf mass basis (data not shown). The observed relationships were not significantly influenced by the variation in SLA, when SLA was included in a multiple regression.

Chlorophyll concentrations were positively correlated with leaf N concentrations, when compared across families and sites (Figure 3.7). The slope of linear relationship was significantly greater for the lower crown than for the upper crown positions (Figure

3.7). Thus, 26 and 15% less leaf N was incorporated into chlorophyll at the upper and middle crown positions, respectively, than in the lower-crown foliage (data not shown).

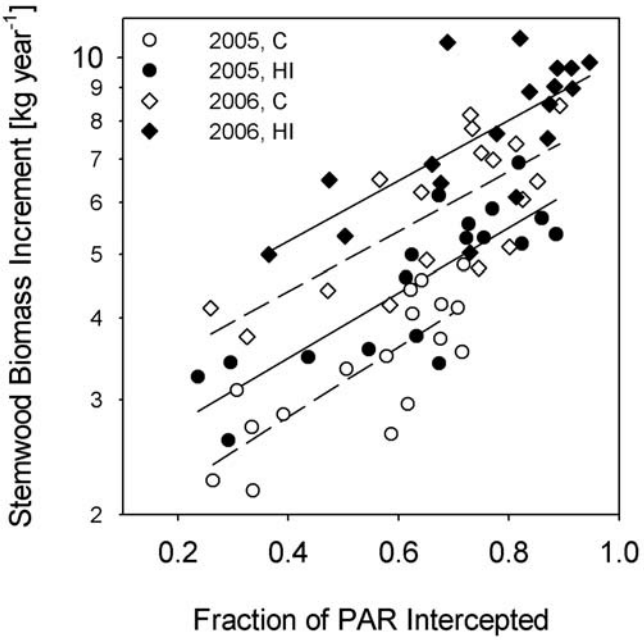

Figure 3.8. Relationships of annual stemwood biomass increment per tree with the plot-level interception of photosynthetically active radiation (PAR) in examined families of loblolly and slash pine. Shown are means for individual plots at two experimental sites in the West Gulf Coastal Plain area; n = ranges from 3 to 6 for each point. Solid lines represent linear fits across two species and sites in the high intensity treatment in 2005 ($\ln Y = 0.78 + 1.15X$, $r^2 = 0.69$, $P < 0.0001$) and 2006 ($\ln Y = 1.23 + 1.06X$, $r^2 = 0.50$, $P = 0.0010$). Dashed lines represent fits for the control treatment in 2005 ($\ln Y = 0.55 + 1.22X$, $r^2 = 0.64$, $P = 0.0001$) and 2006 ($\ln Y = 1.06 + 1.05X$, $r^2 = 0.54$, $P = 0.0008$).

We found no statistically significant relationship between current annual stem increment and any of the leaf-level physiological parameters. Yet, a strong relationship was found between tree growth and the plot-level fraction of intercepted PAR in both growing seasons (Figure 3.8). Stem mass increments per unit intercepted PAR were higher in 2006 than in 2005 for all examined families. Slopes and intercepts did not

differ between species in 2005, but intercepts were different for the two pine species in 2006 (data not shown). Moreover, in both growing seasons, intercepts were higher for the HI treatment than for control treatment, when fitted across sites and families (Figure 3.8), and slopes were not different for cultural treatments or years.

3.5. Discussion

3.5.1. Tree growth and stand development

Several trends observed in the present study reflected changes within the crowns resulting from canopy closure in rapidly developing stands of loblolly and slash pine. These effects of crown development during the fourth and fifth growing seasons were noticeable especially at the Kirbyville site, where trees were larger compared to DeRidder site. Crown recession from the lower tree trunk was visible from an increase in the height to live crown and the dynamic response of crown diameter, as lower branches died and maximum crown diameter moved to higher positions along tree stems. Crown growth dynamics indicated that our stands most likely were approaching maximum crown diameter determined by stand stocking, as crown diameter growth slowed and converged in the two pine species at the end of the fifth growing season. However, no slowing trend in tree growth was found, as the stemwood biomass increment was higher in the fifth than in the fourth growing season. This implies that growth in those stands was still increasing, as they perhaps did not reach their maximum leaf area index yet (Gholz and Fisher, 1982; Ryan et al., 1997).

3.5.2. Leaf morphology and chemistry

In our experiment we observed a pronounced increase in SLA with increasing canopy depth from the upper to lower crown positions. Many other studies reported similar trends in forest canopies (Ellsworth and Reich, 1993; Niinemets et al., 1998;

Meir et al., 2002; Niinemets et al., 2002; McGarvey et al., 2004; Iio et al., 2005), attributing the change in SLA with canopy depth to an increased ability to capture light at lower light intensities with greater leaf area for a given fraction of leaf biomass. The leaf N_a gradient observed within crowns in our experiment is consistent with trends reported from other studies in forest canopies (Bond et al., 1999; Niinemets et al., 2002; McGarvey et al., 2004). For N_m, similar changes along tree crowns as in our study, were also found in *Pinus radiata* D. Don. (Livingston et al., 1998), *Pinus palustris* Mill. and *P. taeda* (Niinemets et al., 2002), but leaf N_m remained relatively constant throughout a light profile within the canopy in *Pinus virginiana* Mill. (Niinemets et al., 2002) or in broadleaved species (Ellsworth and Reich, 1993; Iio et al., 2005).

Changes in SLA and foliar N in slash pine crowns were significant in the fifth, but not in the fourth growing season. In loblolly pine canopies, the trends were also steeper in 2006 than in 2005, and were more pronounced than in slash pine in both years. Thus, observed changes in leaf morphology and biochemistry were most likely associated with a changing light environment in concert with canopy development within the examined stands. Crowns of loblolly pine families were wider and longer than those of slash pine family, thus they intercepted more light. We found linear relationships of leaf N with chlorophyll concentration. Also, per given leaf N concentration, more N was incorporated into chlorophyll in the foliage that developed in shaded conditions of the lower-crown than in needles from upper crown position, which is an acclimation response for more effective light harvesting (Lambers et al., 1998).

The results of models of canopy photosynthesis in tree (Bond et al., 1999), shrub (Field, 1983) and perennial plant canopies (Hirose and Werger, 1987; Pons et al., 1989) show that reductions in N concentration and distribution within canopy might be associated with optimization of photosynthesis at the canopy level. Yet, canopy carbon gain is usually about 10% less under actual N distributions observed in the canopies, than for modeled distributions where N is preferentially allocated to well-lit crown positions based on the optimization theory (Field, 1983; Pons et al., 1989; Bond et al., 1999). De Pury and Farquhar (1997) argued that such a distribution of nitrogen might be

not related to the maximization of canopy photosynthesis at a given instant, because the instantaneous and time-averaged or spatially averaged light conditions vary considerably within crowns. As presented in our study, the distribution of leaf N and A_{max} seemed to acclimate to the spatially averaged irradiance, indicating that perhaps CO_2 assimilation is tuned at canopy level to approach optimum when light environment is spatially integrated.

3.5.3. Leaf-level photosynthesis

Families generally varied little in the leaf-level photosynthesis rates and we did not observe significant differences between two examined pine species, except for A_m of the upper crowns. The lack of differences in leaf-level CO_2 assimilation between loblolly and slash pine is in line with results reported from studies on seedlings (Samuelson, 2000) and trees in 4-year-old stands (Will et al., 2001), but in contrast to another plantation study at a similar age (McGarvey et al., 2004).

In our study carbon assimilation rates decreased with increasing canopy depth at DeRidder, but not at the Kirbyville site. In other studies of loblolly pine, leaf area-based net photosynthesis was higher for upper-crown than for lower-crown foliage (Gravatt et al., 1997; Tang et al., 1999; 2003; Gough et al., 2004b), although not in all cases (Blazier et al., 2004; McGarvey et al., 2004). Results on within-crown variability in assimilation rates for slash pine are much scarcer in the literature, but McGarvey et al. (2004) reported no differences in A_a between upper and lower crown foliage at age 4 years. Our findings generally confirm the ability of loblolly pine needles to acclimate to increased shading (Zhang et al., 1997; Niinemets et al., 2002) and also indicate such an ability for slash pine. Yet, factors other than light may limit photosynthesis when comparing sites and through time, including differences in water availability. Stomatal conductance to water vapor and C_i/C_a ratio were lower at Kirbyville than at DeRidder, thus trees at Kirbyville may have experienced greater water stress. Further investigation of

photosynthesis rates under a range of environmental conditions may be necessary to characterize potential dynamic responses.

3.5.4. Photosynthesis-foliar nitrogen relationship

Although light-saturated photosynthetic rate decreased from upper to lower crown portions, it was only weakly correlated with the gradient in leaf N. Both positive correlations of leaf-level photosynthesis with foliar N (Gough et al., 2004a; McGarvey et al., 2004) and a lack of relationship (Teskey et al., 1994; Zhang et al., 1997; Will et al., 2001; Munger et al., 2003; Gough et al., 2004b) were reported for southern pines. Based on our results, SLA seemed not to be useful in explaining variation in the A_{max}-N relationship within or among these two pine species. We have not observed the general positive inter-relationship between SLA and leaf mass-based photosynthesis and nitrogen, reported from studies involving multiple species and sites (Reich et al., 1997; Reich et al., 1998; Wright et al., 2004). In fact, the correlation of SLA with N_m was negative in our study, due to the opposite trends in both traits within canopies (see Figure 2.4), and there was no relationship between SLA and A_m.

We have not found significant changes in the instantaneous photosynthetic nitrogen-use efficiency within crowns of the two pine species. However, given the gradients in foliar N and photosynthesis, iPNUE based on light-saturated photosynthetic rates should stay relatively stable among canopy positions that represent different growth-light conditions (Poorter and Evans, 1998).

3.5.5. Cultural treatment effects

The high intensity silvicultural treatment, comprised of fertilization and control of competing vegetation, had generally small effects on leaf morphology, biochemistry and physiology in our experiment. In other studies with southern pines, fertilization usually increases concentrations of leaf N (Teskey et al., 1994; Martin and Jokela, 2004a; Sword Sayer et al., 2004). However, at both cultural treatments in our study,

foliar N in general remained above the critical concentrations of 12 mg g^{-1} reported for loblolly pine and 10 mg g^{-1} for slash pine (Jokela, 2002; Gregoire and Fisher, 2004) in the middle and upper-canopy foliage. It should be noted that the control treatment also received fertilization at the time of establishment, a common forestry practice in the Southern US. The effect of fertilization would perhaps be stronger the control was based on the native soil fertility. Moreover, the effect of fertilization on leaf N status is often transient and may not be detected after about 50 days after fertilizer application in loblolly pine (Gough et al., 2004a). Our findings are consistent with this observation as the only significant differences were observed after about one month after fertilization in 2005, and sites were not fertilized in the 2006 growing season.

Leaf-level gas exchange was affected by cultural treatment only at the Kirbyville site, where A_a was reduced in the high intensity treatment when compared with the control, although the level of response depended on family (family × treatment interaction). Published results on the effects of fertilization on leaf-level photosynthesis in southern pines provide mixed results. Net photosynthesis was higher in fertilized trees than in control treatments (Teskey et al., 1994; Murthy et al., 1997; Samuelson, 2000) or the effect differed with time following fertilization (Murthy et al., 1996; Gough et al., 2004a). Also no difference in CO_2 assimilation between fertilized and non-fertilized trees (Zhang et al., 1997; Tang et al., 1999; Samuelson et al., 2001) or inconsistency in the direction of response to fertilization have been reported (Munger et al., 2003; Gough et al., 2004b). Thus, our hypothesis about steeper gradients of leaf N and photosynthetic capacity in the HI treatment in response to increased shading was not supported, although the lower canopy was more deeply shaded in the HI than in the C treatment.

3.5.6. Implications for canopy photosynthesis and tree growth

Tree growth was correlated with the fraction of PAR intercepted at the plot level in our study. This is in agreement with other studies reporting a similar relationship (Cannell, 1989; Dalla-Tea and Jokela, 1991; Will et al., 2005). A common slope of the relationship for all families suggests that both pine species may have similar light-use

efficiency for growth (Will et al., 2001). However, at given level of intercepted PAR, loblolly pine trees grew more than slash pine in 2006. This may indicate divergence in growth between the two species with stand age (Shiver, 2002).

The effect of cultural treatment on crown size in our study was weak, but the intercepts of relationship between stemwood increment and intercepted PAR were higher in the high intensity treatment than in the control in both growing seasons. The intercepts of that relationship varied from 1.73 to 3.42 kg $year^{-1}$ (see Figure 3.8), indicating a shift in the elevation of the relationship over the data range. Fertilization usually increases stand foliage biomass and leaf area index in southern pines (Vose and Allen, 1988; Colbert et al., 1990; Gillespie et al., 1994; Albaugh et al., 1998; Jokela and Martin, 2000; Will et al., 2002). We did not quantify leaf area in our stands, but differences between treatments in the iPAR were small, except at DeRidder site in 2005 for slash pine, suggesting that the treatment effect on leaf area was rather small in our study. The higher intercepts of the relationship between tree growth and iPAR for the HI imply increased growth efficiency of needles (Waring, 1983) in the high intensity treatment, whereas light-use efficiency (slope) remained the same in both treatments. On the other hand, between-species differences associated with accumulated leaf area most likely have a larger influence on observed differences in tree growth between loblolly and slash pine than differences in leaf-level photosynthetic rates (Will et al., 2001; McGarvey et al., 2004).

We found no relationship between tree growth, and leaf-level photosynthetic rates, which supports other findings that show the lack of a strong relationship of plant growth with assimilation rates at leaf level (Elmore, 1980; Poorter, 1989; Poorter and Van der Werf, 1998). Though, when CO_2 assimilation rate is integrated and expressed on a plant mass basis the correlation with growth rate improves considerably (Kruger and Volin, 2006). Thus, integrating leaf area, light interception and photosynthesis at the canopy scale may be a better approach to link tree growth with carbon assimilation than comparing measurements on one or more dates.

Crown structure, which governs leaf area distribution, was likely responsible for observed differences in light interception and tree growth. Both loblolly pine families in our experiment had larger crowns and more leaf area than the slash pine family at age 2 years (Chmura et al., 2007). At that time, leaf area density (amount of leaf area per crown volume, $m^2\ m^{-3}$) was higher in slash pine than in loblolly pine at a given crown size; therefore, slash pine might exhibit more within-crown shading than loblolly pine before canopy closure (Oker-Blom and Kellomaki, 1983; Kuuluvainen and Pukkala, 1989). The crowns were still larger for loblolly pine families in the present study, and intercepted more light at the plot level than the slash pine family. Thus, canopy carbon assimilation, affected by crown size and structure and leaf area distribution, may differ in the examined families of loblolly and slash pine.

Our findings indicate that integration of leaf-level assimilation rates to the whole canopy should take into account variability in leaf morphological and physiological properties within tree crowns as affected by light availability (Niinemets et al., 1998; Meir et al., 2002). Our point-in-time measures of leaf photosynthetic rates demonstrate that light environment is the main factor governing CO_2 assimilation as well as leaf traits within examined tree crowns, and thus may be of use in informing modeling efforts of canopy photosynthesis.

4. LINKING CROWN AND CANOPY TRAITS TO LIGHT ABSORPTION AND STAND GROWTH IN FAMILIES OF LOBLOLLY AND SLASH PINE

4.1. Overview

Forest productivity is inherently related to absorbed light (APAR – absorbed photosynthetically active radiation). Crown size, leaf area and its distribution within crowns affect APAR and photosynthesis at the canopy level, which may lead to differences in aboveground productivity. Light-use efficiency (ε), an integrative trait linking biomass growth and intercepted light, is useful in modeling stand growth. To assess how genotype and silvicultural treatment affect ε in southern pines, we simulated annual APAR and canopy photosynthesis with the process-based model MAESTRA in young stands of six selected families of loblolly pine (*Pinus taeda* L.) and one slash pine (*Pinus elliottii* Engelm.) at the onset of canopy closure, under two contrasting silvicultural treatments in the West Gulf Coastal Plain of Louisiana.

We found pronounced differences in aboveground growth and canopy light absorption and photosynthesis among examined families. Among all families and treatments, aboveground biomass productivity was positively but non-linearly related to APAR and canopy photosynthesis. Light-use efficiency varied among families from 0.41 to 0.56 g MJ^{-1}, with slash pine having the lowest ε. Families with more leaf area, larger crowns, and low leaf area density per crown volume absorbed the most light and grew the most. Silvicultural treatment did not significantly affect aboveground growth, crown traits, vertical leaf area distribution and light absorption parameters, although these traits generally ranked higher in the treatment receiving fertilization and vegetation control than in the control treatment. The observed variability in aboveground biomass growth among families was related more to total stand leaf area and APAR than to differences in light-use efficiency at this stage of stand development. Physiological attributes are better predictors of family performance when integrated to the canopy level than the instantaneous leaf-level measurements of net photosynthesis in the examined pine

species. These findings may be useful in establishing selection criteria for the most productive genotypes and in modeling productivity in intensively managed pine plantations.

4.2. Introduction

Forest growth reflects the combined effects of genetics and environment on physiological and morphological properties and allocation patterns integrated from the levels of individual organs to trees and stands. Tree growth and stand production depend on carbon assimilation in photosynthesis. Although photosynthesis governs carbon acquisition by plants, the correlations of leaf-level photosynthetic rates with plant growth are usually weak (Elmore, 1980; Poorter, 1989; Lambers et al., 1998). The lack of a general relationship of tree growth with leaf photosynthetic capacity points toward the importance of integrating physiological processes and attributes of leaves within crowns for understanding the relationship of forest production with carbon assimilation (Kruger and Volin, 2006).

One of the major factors affecting photosynthesis is light. Light environment in forest canopies is highly heterogeneous due to variation in the amount of leaf area, its distribution within crowns, and the temporal dynamics of solar insolation. However, even within tall forest canopies, leaves in sun-flecks experience high light intensities for some periods during the day (Gay et al., 1971; Zavitkovski, 1982; Pearcy, 1990). In conifer tree species, relatively more direct beam-light penetrates into deeper canopy layers due to the greater degree of clumping of foliage around shoots compared to canopies with a more random or uniform leaf area distribution (Oker-Blom and Kellomaki, 1983; Whitehead et al., 1990; Gholz et al., 1991; Stenberg et al., 1994). The relationships between crown structural traits, light absorption, and productivity differences within and among pine species are not fully understood.

A positive linear relationship of intercepted radiation with aboveground production is often observed in trees (Cannell, 1989; Dalla-Tea and Jokela, 1991;

McMurtrie et al., 1994; McCrady and Jokela, 1998; Will et al., 2001), despite a strongly non-linear response of leaf photosynthesis to light intensity (Stenberg et al., 1994; Medlyn et al., 2003). The relationship of biomass accumulation with light interception is ultimately affected by the effectiveness of incorporating assimilated carbon into biomass, which is referred to as radiation- or light-use efficiency (ε). Values of ε vary from 0.27 to 1.6 g dry mass MJ^{-1} absorbed photosynthetically active radiation (APAR) among pine species of various climatic zones (Stenberg et al., 1994). When compared in the same stands, family and species differences in light-use efficiency have been shown to exist (Dalla-Tea and Jokela, 1991; Stenberg et al., 1994; McCrady and Jokela, 1998). McCrady and Jokela (1996; 1998) concluded that differences in light-use efficiency among families of loblolly pine must be coupled with crown structural properties to elucidate the effect of light interception on stand productivity. They found that loblolly pine genotypes which displayed above 60% of their leaf area in the mid-crown intercepted more light and had greater ε compared to families with more uniform leaf area index (LAI) distributions with canopy depth (McCrady and Jokela, 1996). However, the effect of intensive silvicultural treatment on light-use efficiency is not well resolved, despite large effects of fertilization and weed control on LAI in loblolly and slash pine stands (Dalla-Tea and Jokela, 1991). Martin and Jokela (2004b) suggested that changes in ε might be affected both by stand development and nutrient availability. The concept of ε is especially attractive, because if light-use efficiency values were readily available, estimation of stand aboveground productivity would be easily predicted by the multiplication of ε by intercepted light.

The direct measurement of gas exchange in forest canopies is difficult, although possible with the use of micrometeorological methods (Norman and Hesketh, 1980; Baldocchi et al., 1988). To this point, process-based models are invaluable tools for scaling physiological processes from individual leaves to crowns and canopies and for improving our understanding of the factors related to scaling. The heterogeneity of forest canopies and the non-linearity in response of physiological processes to the driving variables pose special challenges (Jarvis, 1995; Medlyn et al., 2003). A number of

models that differ in complexity, required input data and spatial and temporal resolution of output are available to estimate light interception and stand-level carbon assimilation and growth (McMurtrie et al., 1994; Medlyn et al., 2003). Models range from simple big-leaf models (Evans and Farquhar, 1991) to those that divide leaf area into sunlit and shaded fractions, or more complex models that divide the canopy into several layers with different leaf angle classes (Norman, 1980; Boote and Loomis, 1991; Cropper and Gholz, 1993; Norman, 1993; McMurtrie et al., 1994; De Pury and Farquhar, 1997; Medlyn et al., 2003). The use of a particular model should be ultimately dictated by the modeling objectives and availability of input data (Medlyn et al., 2003).

The MAESTRA model (Medlyn, 1998) is a modification of a canopy light interception and carbon assimilation model, MAESTRO (Wang and Jarvis, 1990a). The model has been successfully applied to simulate light absorption and canopy carbon uptake in a number of species, including Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Wang et al., 1991), Norway spruce (*Picea abies* (L.) Karst.) (Ibrom et al., 2006), and loblolly and slash pine (Baldwin et al., 1993; Luo et al., 2001; Emhart et al., 2007). To date, the questions addressed with the model have ranged from comparisons of model output with direct measurements of canopy carbon uptake (Luo et al., 2001; Ibrom et al., 2006) to the determination of the effects of canopy structure on light interception (Wang and Jarvis, 1990b; Emhart et al., 2007), the relationship of light absorption with stand growth (Wang et al., 1991; Luo et al., 2001), and the effects of climate change on carbon gain (Cropper et al., 1998). In our study, we simulated canopy light interception and photosynthesis in young stands of loblolly and slash pine families differing in productivity and crown size (Chmura et al., 2007; Chmura and Tjoelker, *in press*) to assess how genotype and silvicultural treatment affect light-use efficiency in southern pines.

Loblolly pine and slash pine are native to the Southeastern United States and are widely planted throughout the region. Most planting material in both species is genetically improved and obtained from tree breeding programs (McKeand et al., 2003; McKeand et al., 2006). Between- and within-species differences have been observed in

aboveground biomass accumulation (Colbert et al., 1990; McCrady and Jokela, 1998; Jokela and Martin, 2000; Jokela et al., 2000; Roberts, 2002; Shiver, 2002; Martin and Jokela, 2004b; Roth et al., 2007) and crown architecture (McCrady and Jokela, 1996; Xiao et al., 2003a; Chmura et al., 2007; Emhart et al., 2007). Yet, the interrelationships between crown structure, light interception, and productivity among genotypes are not fully understood.

Deployment of genetically improved planting material should ideally be coupled with intensive silviculture to achieve high returns from forest sites (Allen et al., 2005). The most effective form of site manipulation in the Southern US is fertilization coupled with control of competing vegetation (Allen et al., 1990; Allen et al., 2005). Fertilized stands of loblolly and slash pine are more productive than unfertilized ones (Jokela et al., 2004), especially on nutrient-deficient soils, and where water availability is not a limiting factor (Jokela et al., 2000; Jokela, 2002). Improved productivity may result from increased leaf area and changed patterns of biomass allocation. In pines, leaf biomass and leaf area index usually increase in concert (Vose, 1988; Colbert et al., 1990; Gillespie et al., 1994; Vose et al., 1994; Jokela and Martin, 2000), and proportional biomass allocation to roots may decrease in response to fertilization (Samuelson et al., 2004). As a consequence, more fixed carbon might be allocated to the production of stem-wood and new leaf area. Thus, increases in leaf area, light interception and canopy carbon gain are likely the cause of improved growth of fertilized stands (Jokela and Martin, 2000; Martin and Jokela, 2004b), rather than differences in leaf-level photosynthetic rates between intensively managed and control stands (Zhang et al., 1997; Tang et al., 1999; Chmura and Tjoelker, *in press*).

In the present study we investigated aboveground growth in stands of six selected families of loblolly pine and one of slash pine under two contrasting silvicultural treatments during the fourth growing season in the field. We examined how crown development at the onset of canopy closure affects light interception and stand productivity. We used the process-based model MAESTRA (Medlyn, 1998) to determine light absorption and canopy photosynthesis. The specific objectives of our

study were: (i) to determine light interception and photosynthetic carbon gain at the tree and canopy scale and relate it to aboveground productivity in pine stands, and (ii) to determine how the relationship of intercepted radiation with aboveground growth may vary with genotype, silvicultural treatments, and possible genotype × treatment interaction effects.

4.3. Materials and Methods

4.3.1. Experimental site

The research site is located in the West Gulf Coastal Plain in DeRidder, Louisiana (30º 51' N, 93º 21' W) and constitutes a part of the PPINES experiment (Pine Productivity Interactions on Experimental Sites), established by the Forest Biology Research Cooperative at the University of Florida. The long-term (1971-2000) mean annual air temperature is 19.3 °C, and mean annual precipitation is 1560 mm with a monthly maximum in December at 169 mm and minimum in August at 106 mm (NOAA, 2002b). Air temperatures during the study period (February 2005 – February 2006) were generally representative of the long-term mean, except the mean temperatures for September 2005 and January 2006 were 2.7 and 3.7 °C warmer than average, respectively. The period between March and June 2005 had 30 to 81 mm lower precipitation than the long-term mean, and September 2005 had 241 mm more rainfall than an average for the area (http://www.noaa.gov). The soil at the site is a somewhat poorly drained fine-silty, siliceous, active, thermic Typic Glossaqualf of the Caddo series (http://websoilsurvey.nrcs.usda.gov).

The experiment was established in a split-plot design in five randomized complete blocks. The main-plot treatment consisted of two contrasting silvicultural treatments: control (C) with fertilization (50.5 kg ha^{-1} N and 55.5 kg ha^{-1} P applied as 280.5 kg ha^{-1} of diammonium phosphate) and control of competing vegetation with Arsenal® (imazapyr) and Garlon™ (triclopyr) applied only at the time of site

establishment, and high intensity (HI) with complete vegetation control and fertilization on a regular basis, beginning in the second growing season. The need for fertilizer additions was guided by yearly analyses of foliar nutrient concentrations, based on critical levels given in Gregoire and Fisher (2004). The cumulative elemental rates (kg ha^{-1}) applied though the fourth growing season reached 303 N, 123 P and 66 K. Mg, Ca, S, B and Cu were applied at 26.9, 32.5, 60.6, 0.4 and 3.4 kg ha^{-1}, respectively. One replication was excluded from the study, because one family was not represented there and the cultural treatment was not applied to that block at age four years. Thus, our study is comprised of four replicate blocks.

Five elite families of loblolly pine, one of slash pine, and one poorer-growing loblolly pine family were randomly assigned as sub-plots within cultural treatments. The experimental site was established in January 2002. Containerized seedlings were planted in a 2.4 × 3.3 m spacing (1,223 trees ha^{-1}) in 0.0588 ha pure-family plots (72 trees $plot^{-1}$) where the inner 42 trees constituted the measurement plot (0.0343 ha). Details on site preparation and planting material are given in Chmura et al. (2007).

4.3.2. Measurements

Stand inventory measurements were collected at the end of the third (2004) and fourth (2005) growing seasons. Diameter at breast height (1.3 m, DBH) was measured on all trees in both years. Tree heights were measured for all trees in 2004. In the fourth growing season, tree heights were measured on a subset of trees of each plot and heights were subsequently fitted for all trees using linear regression relationships between DBH and tree height for each family ($r^2 > 0.83$, $P < 0.0001$). Survival since planting averaged 87% for the experimental site. Fifteen trees that died during the 2004-05 study period were excluded from the analysis.

Crown traits were measured during the fourth (2005) growing season in the field (Chmura and Tjoelker, *in press*) in three of the seven families, Lob 1 (an average-growing family), Lob 5 (the most productive family) and Slash 6, which were also used

in a study of allometric relationships and crown structure at age two years (Chmura et al., 2007). Based on a stratified random sample, six trees in each family plot were chosen to represent the range of tree sizes in each treatment combination in each of three of four replicate blocks. In total, we sampled 108 trees (6 trees / 3 families / 2 cultural treatments / 3 blocks). Crown traits included height to live crown, crown length, and crown diameter at the widest point in two directions (parallel and perpendicular to planting beds). Based on the linear regression relationships with DBH (Table C.1) developed for the sampled trees, crown radii were fitted for all measured trees of all seven families in all four blocks of the experiment. Regression relationships of height to live crown with DBH or tree height were statistically weak. Thus, an average value for species or family within cultural treatment was used for height to live crown in the model simulations. Canopy cover was calculated as the ratio between the projected area of crowns per plot and plot area.

Plot-level PAR (photosynthetically active radiation; 400-700 nm waveband) interception was measured with a 1-m long line quantum sensor (LI-191, LI-COR, Lincoln, NE, USA). Measurements were taken 1 m above the ground under the canopy on three or four non-overlapping 22-m-long transects with 12 points each within each plot, which provided a spatially averaged measure of light interception. Below-canopy measurements were referenced against a cross-calibrated PAR sensor placed outside the stand in an open area and recording instantaneous values every 30 s. All seven families in all four blocks in the experiment were measured on a single sunny day (October 14, 2005) during a 4-hour period centered on solar noon. These direct measurements of plot-level PAR interception were compared with estimates of PAR absorption simulated by the MAESTRA model for the same date and time of day.

4.3.3. Model description and parameterization

We used the MAESTRA model (Medlyn, 1998) to simulate light absorption and canopy photosynthesis. The canopy was divided into six layers and light interception

was simulated for 12 grid-points within each layer for each tree. As inputs, the model requires the position of individual trees in *x* and *y* coordinates together with crown radii, crown length, height to live crown, leaf area per tree, and leaf area distribution (see below). Meteorological data recorded at the site and used in our simulation were air temperature (°C), relative humidity (%) and above-stand PFD (μmol m^{-2} s^{-1}, PAR) at half-hour time steps during the simulation period. Crown shape was described as 'round', which assumes a full ellipsoid crown shape and is in agreement with our field measures (Appendix D). Leaf-level physiological parameters for both pine species were based on a literature survey and our own field measures (Table C.2). The Ball-Berry model of stomatal conductance response to relative humidity, with parameters given in Luo et al. (2001) was used in our simulations. The 12-month simulation period began February 17, 2005 and ended February 17, 2006, representing the fourth growing season in the field, which included periods regarded as non-growing (December through February). Monthly and annual estimates of PAR absorption (APAR; MJ m^{-2} ground area) and canopy net photosynthesis (total photosynthesis subtracting foliar maintenance respiration; mol m^{-2}) were derived by summation of daily outputs from the model and expressed per ground area. Hourly measures of APAR in μmol were converted to MJ given 4.57 mol PAR MJ^{-1} (McCartney, 1978). Stem wood biomass was calculated from the relationship between tree height, DBH and wood dry-mass, presented in Nemeth (1973). Biomass of all aboveground components was summed to obtain total aboveground biomass per unit of ground area, and light-use efficiency (ε) was estimated as the ratio between aboveground biomass increment and APAR for each experimental plot.

Leaf biomass per tree was estimated for all trees measured during the inventory at age three and four years with the regression of foliage biomass on tree DBH (Table C.1). Allometric relationships were developed on site for trees harvested at age two years (Chmura et al., 2007) and at age six years (see section on leaf area distribution). To obtain equation parameters - intercepts and slopes - for ages three and four years, values of foliage biomass were regressed against DBH for 18 individual trees at age two and six

years, and the parameters were estimated for the intermediate years, assuming a linear interpolation of the parameter estimates. Total projected leaf area per tree for the model input was determined for each foliage age cohort (see below) by multiplying total foliage mass per tree by the proportion of each needle age class and corresponding median SLA (specific leaf area, $m^2 kg^{-1}$) for a species and foliage age class.

A similar procedure as for leaf biomass was used for the determination of branch biomass per tree, except that a single relationship was fit for tree ages 2 and 6 years for each species (Table C.1). We calculated crown volume (m^3) assuming an ellipsoid crown shape and estimated leaf area density (LAD, $m^2 m^{-3}$) and branch mass density (BMD, $kg m^{-3}$) per crown volume.

4.3.4. Leaf area distribution

In our simulations, leaf area distribution in the horizontal direction was assumed to be uniform. To determine the vertical distribution of leaf area, branch samples were collected in July 2007. We sampled 18 trees from the same three families, chosen to represent the range of tree sizes for family and cultural treatment. On each tree we measured height, DBH and heights to each whorl. Using tree-climbing ladders, we measured the basal diameters of all live branches with a caliper to the nearest 1 mm. A representative sample of branches (6-13 branches per tree) along the length of the tree crown was cut from every tree. Branch lengths were recorded, and needles from two age cohorts (current and previous year) were collected separately for dry mass determination. Each foliage age cohort may include more than one flush formed during the previous and current growing season. In the field, sub-samples of current and previous year needle age classes were taken from each branch and kept on ice for SLA determination. These needles were scanned on a flatbed scanner in the laboratory and projected leaf area was determined with WinRhizo software (Regent Instruments Inc., Canada).

Foliage and branch samples were dried at 75 °C to determine dry-mass. Subsequently, leaf area per branch (m^2, projected) was estimated by multiplying foliage dry mass of each sampled branch by its corresponding SLA value. Leaf area per branch was then used to determine parameters of the following non-linear equation (Xu and Harrington, 1998):

$$BL_a = aBD^b \exp(cRHIC^d) \quad (4.1)$$

where BL_a is leaf area per branch (m^2), BD is branch diameter in mm, RHIC is relative height in crown at the branch origin (ranging from 0 (bottom) to 1(top)), and *a, b, c* and *d* are the fitted parameters. The fitted parameter values derived from equation 4.1 (r^2 = 0.87, $P < 0.0001$) were used to predict the total leaf area per branch for all branches on each sample tree, based on measured branch diameter and relative height. Total leaf area per branch was divided into two foliage age classes by multiplying branch leaf area by the proportion of each age class, described with the following equations:

$$CL_a = g + hRHIC + i(RHIC\text{-}j)^2 \quad (4.2)$$

$$PL_a = 1 - CL_a \quad (4.3)$$

where CL_a and PL_a are the current and previous year leaf area proportions of total branch leaf area, respectively, and *g, h, i* and *j* are the estimated parameters and RHIC as defined above. Parameters for equations 4.1 and 4.2 ($r^2 > 0.73$, $P < 0.0001$) are presented in Table C.3.

The crowns of the sampled trees were divided into 12 horizontal layers and vertical leaf area distribution for each foliage age cohort was estimated with a beta function (Wang et al., 1990):

$$f(RH_L) = kRH_L^m (1\text{-}RH_L)^n \quad (4.4)$$

where $f(RH_L)$ is the leaf area of a layer at RH_L relative height within a crown, and *k, m* and *n* are the fitted parameters. We estimated parameters separately for current-year and previous-year foliage distributions for each sample tree (Table C.4). Leaf area must be normalized by dividing by total leaf area, so that the integral of $f(RH_L)$ from $RH_L = 0$ to 1 is equal to 1 (Wang et al., 1990).

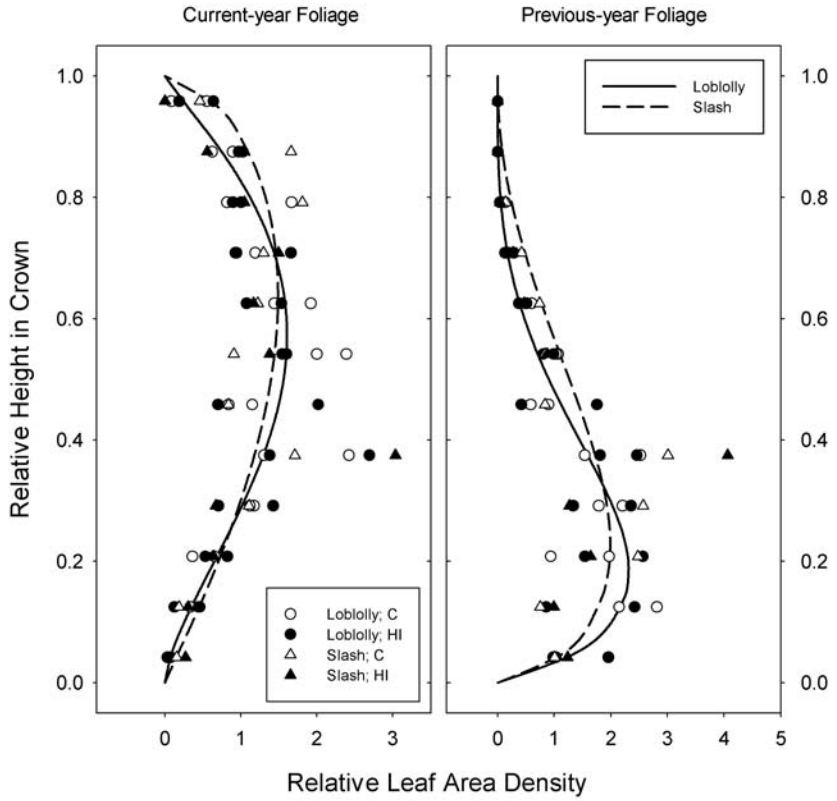

Figure 4.1. Vertical leaf area distribution for two age classes of foliage in loblolly and slash pine families. The canopy was divided into 12 layers; values are shown at heights representing the midpoint of each layer. Each point at a given height represents the mean of up to three sampled trees in each family. Closed symbols represent the high intensity treatment (HI) and open symbols - the control (C). Lines show beta function fits (see Table C.4).

Our approach assumes that the leaf area of a branch is distributed close to the measured height of the branch base along the stem, which does not account for differing branch angles within crowns. However, dividing crowns into multiple layers alleviates

this problem (Maguire and Bennett, 1996). The median values of estimated parameters for needle age cohort and species (Table C.4, Figure 4.1) were used to describe the vertical leaf area distribution for all trees in the simulation.

4.3.5. Crown growth in simulations

Light absorption in the model is simulated based on crown dimensions and the amount and distribution of leaf area. Crown size and leaf area are assumed to change linearly between the beginning and the end of study if the start and end values are provided as inputs. We reasoned that the annual estimates of APAR would differ if mid-season crown size and leaf area measures were included, owing to non-linear crown growth through the course of a growing season. Therefore, using two crown development scenarios – linear and mid-season, we modeled annual light interception for the three families for which tree and crown parameters were determined mid-season in July 2005 (Chmura and Tjoelker, *in press*).

4.3.6. Analysis

Analysis of variance was used to test for cultural treatment and family effects on aboveground biomass and its annual increment at the plot level. The block × cultural treatment was used as an error term for treatment effect using *F* tests, and the residual error was used for family and family × treatment interaction effects (see Table 4.1). APAR and canopy net photosynthesis were each analyzed as an annual sum, and as monthly sums and analyzed by month using analysis of variance. Linear regression was used to analyze relationships between traits. All effects were considered significant at the probability level $P \leq 0.05$. JMP 5.0.1 statistical software (SAS Institute, Cary, NC, USA) was used to conduct all analyses.

4.4. Results

4.4.1. Tree growth and aboveground productivity

Annual aboveground biomass production during the fourth growing season differed among the seven examined families (Table 4.1). The most productive family (Lob 5) had almost two times greater aboveground biomass and stemwood increment as the slowest-growing loblolly pine family (Lob 7), and more than two-fold greater production than the slash pine family (Table 4.1). The ranking of families in terms of aboveground biomass remained the same in both years.

Cultural treatment had no significant effect on the aboveground and stemwood biomass and their current annual increments, and there were no significant family × treatment interactions (Table 4.1). However, the growth response to the HI treatment varied from a 5% decrease in standing stem biomass at age 3 years for family Lob 1 (the average-growing family), to a 48% increase for family Lob 3 for the same trait. Overall, the mean values ranked higher in the HI treatment than in the control (Table 4.1).

4.4.2. Crown and canopy attributes

Vertical leaf area distribution was similar in both species and did not differ among families (Figure 4.1, Table C.4). Previous-year foliage distribution peaked in the lower third of the crown. The leaf area of current-year foliage peaked between 0.6 and 0.75 of relative height in the crowns of both species (Figure 4.1).

Table 4.1. Mean values (s.e.) of aboveground biomass, stemwood biomass and their annual increments for loblolly and slash pine families during the fourth growing season at the DeRidder experimental site.

		Aboveground Biomass age 3 years		Aboveground Biomass age 4 years		Aboveground Biomass Increment		Stem Biomass age 3 years		Stem Biomass age 4 years		Stem Biomass Increment	
	Family[1)]	[Mg ha^{-1}]		[Mg ha^{-1}]		[Mg ha^{-1} year^{-1}]		[Mg ha^{-1}]		[Mg ha^{-1}]		[Mg ha^{-1} year^{-1}]	
	Lob 5	11.67^{a}	(1.41)	22.36^{a}	(2.51)	10.69^{a}	(1.10)	5.92^{a}	(0.73)	12.16^{a}	(1.34)	6.24^{a}	(0.61)
	Lob 4	10.16^{ab}	(1.30)	19.78^{ab}	(2.46)	9.62^{ab}	(1.17)	5.10^{ab}	(0.68)	10.64^{ab}	(1.33)	5.54^{ab}	(0.66)
	Lob 1	8.42^{abc}	(1.18)	15.89^{bc}	(2.17)	7.47^{bc}	(1.02)	4.15^{bc}	(0.60)	8.52^{bc}	(1.17)	4.38^{bc}	(0.59)
	Lob 2	7.78^{bc}	(0.95)	15.00^{bc}	(1.68)	7.21^{bc}	(0.74)	3.84^{bc}	(0.48)	8.03^{bc}	(0.90)	4.19^{bcd}	(0.42)
	Lob 3	8.73^{abc}	(1.34)	15.25^{bc}	(2.09)	6.52^{c}	(0.77)	4.29^{abc}	(0.68)	8.16^{bc}	(1.12)	3.87^{bcd}	(0.45)
	Lob 7	6.42^{c}	(0.96)	12.17^{c}	(1.63)	5.76^{c}	(0.70)	3.07^{c}	(0.47)	6.37^{c}	(0.86)	3.30^{cd}	(0.40)
	Slash 6	5.68^{c}	(0.96)	10.24^{c}	(1.60)	4.56^{c}	(0.64)	2.63^{c}	(0.46)	5.21^{c}	(0.81)	2.58^{d}	(0.36)
	mean	**8.41**	**(0.49)**	**15.81**	**(0.90)**	**7.40**	**(0.42)**	**4.14**	**(0.25)**	**8.44**	**(0.49)**	**4.30**	**(0.24)**
	Treatment[2)]												
	C	7.49^{a}	(0.59)	14.27^{a}	(1.14)	6.78^{a}	(0.56)	3.70^{a}	(0.31)	7.68^{a}	(0.63)	3.98^{a}	(0.32)
	HI	9.33^{a}	(0.76)	17.35^{a}	(1.35)	8.02^{a}	(0.61)	4.58^{a}	(0.39)	9.20^{a}	(0.73)	4.62^{a}	(0.35)

Source of Variation	**d.f.**	***P* > F**	***P* > F**	***P* > F**	***P* > F**	***P* > F**	***P* > F**
treatment[3)]	1	0.2282	0.2496	0.2824	0.2516	0.2769	0.3111
family	6	**< 0.0001**	**< 0.0001**	**< 0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
fam x treatment	6	0.3363	0.4044	0.5109	0.3309	0.4046	0.5061

[1)] Families are rank-ordered based on aboveground biomass increments. [2)]Silvicultural treatment comparison – C and HI refer to control and high intensity treatments, respectively; values followed with the same superscript letters are not significant for a given trait (family and treatment comparisons) at $\alpha = 0.05$ (Tukey-Kramer test). [3)]Block × cultural treatment with 3 d.f. was used as the error term for treatment effect, and the residual error with 36 d.f. for the other effects.

Crown volume differed significantly among the examined families, with the Lob 5 and Lob 4 families having significantly larger crowns than most other families (Table 4.2). Slash pine always had the lowest values of crown volume among the tested genotypes. Leaf area density (LAD) was inversely related to crown volume; therefore rankings of families in these traits were opposite (Table 4.2). Slash pine had the highest LAD and branch mass density (BMD), which were significantly greater than for any loblolly pine family. Cultural treatment had no statistically significant effect on LAD. Although silvicultural treatment effect on BMD was statistically significant, the difference between treatments was on average only 5% (Table 4.2).

Projected leaf area index (LAI) at the end of simulation period and its annual increment were strongly positively correlated with crown volume. Therefore, family rankings were similar for these traits (Table 4.2). On the individual plot level, LAI ranged from 0.66 to 4.19 m^2 m^{-2}. Cultural treatment effects on crown volume and LAI were not statistically significant, although higher mean values were observed in the HI treatment (Table 4.2). Canopy cover varied among families with little effect of cultural treatment (Table 4.2). Canopy cover is influenced both by crown size and stand stocking. These traits together explained 97% of the variation in canopy cover (data not shown), although the contribution of stocking in a multiple regression was small (8% additional variance explained). Among the individual plots, canopy cover varied from open (0.19; Slash 6) to full-cover (1.30; Lob 5).

Table 4.2. Mean (s.e.) values of crown volume, leaf area density, branch mass density, projected leaf area index (LAI) and its annual increment, and canopy cover for examined families of loblolly and slash pine in the fourth growing season at the DeRidder experimental site.

	Crown Volume		Leaf Area Density		Branch Mass Density		LAI		LAI Increment		Canopy Cover[3)]	
Family[1)]	[m^3]		[m^2 m^{-3}]		[kg m^{-3}]		[m^2 m^{-2}]		[m^2 m^{-2} $year^{-1}$]			
Lob 5	31.22^{a}	(3.26)	0.87^{d}	(0.01)	0.12^{b}	(0.003)	2.95^{a}	(0.30)	1.00^{a}	(0.08)	0.94^{a}	(0.09)
Lob 4	28.99^{ab}	(2.91)	0.94^{cd}	(0.02)	0.12^{b}	(0.003)	2.68^{ab}	(0.31)	0.94^{a}	(0.10)	0.80^{ab}	(0.08)
Lob 2	21.33^{bc}	(2.36)	1.00^{bcd}	(0.01)	0.11^{b}	(0.003)	2.16^{bc}	(0.23)	0.77^{ab}	(0.06)	0.67^{b}	(0.06)
Lob 1	19.96^{c}	(1.97)	1.06^{bcd}	(0.01)	0.12^{b}	(0.003)	2.26^{abc}	(0.28)	0.76^{ab}	(0.08)	0.66^{b}	(0.07)
Lob 3	19.55^{c}	(2.13)	1.07^{bc}	(0.01)	0.12^{b}	(0.003)	2.19^{abc}	(0.28)	0.63^{bc}	(0.06)	0.68^{b}	(0.08)
Lob 7	15.74^{cd}	(1.87)	1.14^{b}	(0.01)	0.12^{b}	(0.002)	1.88^{cd}	(0.24)	0.68^{b}	(0.06)	0.60^{b}	(0.07)
Slash 6	9.02^{d}	(1.58)	1.60^{a}	(0.11)	0.22^{a}	(0.010)	1.23^{d}	(0.17)	0.40^{c}	(0.04)	0.34^{c}	(0.05)
mean	**20.83**	**(1.27)**	**1.10**	**(0.03)**	**0.13**	**(0.0049)**	**2.19**	**(0.12)**	**0.74**	**(0.04)**	**0.67**	**(0.03)**
Treatment[2)]												
C	18.40^{a}	(1.70)	1.09^{a}	(0.04)	0.13^{b}	(0.0063)	1.98^{a}	(0.15)	0.69^{a}	(0.05)	0.61^{a}	(0.04)
HI	23.26^{a}	(1.79)	1.10^{a}	(0.05)	0.14^{a}	(0.0077)	2.40^{a}	(0.18)	0.79^{a}	(0.05)	0.72^{a}	(0.05)

Source of Variation	d.f.	*P* > F	*P* > F	*P* > F	*P* > F	*P* > F	*P* > F
treatment[4)]	1	0.1593	0.8893	**0.0026**	0.2047	0.2655	0.2118
family	6	**<0.0001**	**<0.0001**	**< 0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
fam x treatment	6	0.4917	0.9857	0.6448	0.3470	0.4448	0.2930

[1)] Families are rank-ordered based on crown volume. [2)] Silvicultural treatments as in Table 4.1; values followed with the same superscript letters are not significantly different for a given trait (family and treatment comparisons) at $\alpha = 0.05$ (Tukey-Kramer test). [3)]Canopy cover is the ratio of projected crown area per plot to plot area. [4)]Block × cultural treatment with 3 d.f. was used as the error term for the treatment effect, and the residual error with 36 d.f. for the other effects.

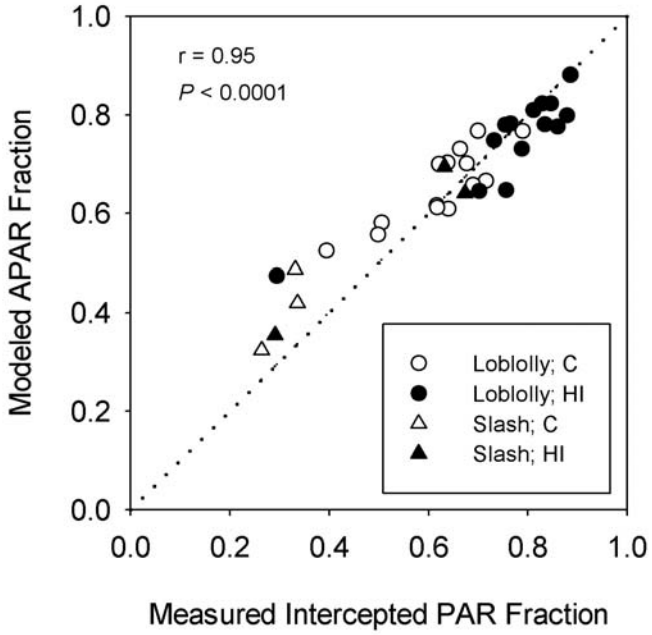

Figure 4.2. Modeled fraction of absorbed photosynthetically active radiation (APAR) per ground area vs. measured values of intercepted PAR in the field at the corresponding solar time on October 14, 2005. The correlation was based on all data across the species and cultural treatments (n = 34 plots). The dotted line shows the 1:1 relationship.

4.4.3. Light interception and canopy photosynthesis

Values of APAR simulated by the model in general agreed well with measured PAR interception at the plot level (Figure 4.2). However, for plots with the fraction of intercepted PAR below 0.5, the model tended to overestimate APAR by up to 38% (Figure 4.2). Light absorption differed significantly among families in each month and overall as annual totals (Table 4.3). During the study period, weekly sums of APAR increased from February to May, then stayed relatively stable until September and peaked in October, followed by decreasing values through January the following year (Figure 4.3). Although the cultural treatment effect on APAR was not statistically significant (Table 4.3), plots in the HI treatment absorbed from 13 to 31% more PAR on

an annual basis than in the C treatment, except for the Lob1 family (Table 4.3). In general, the slash pine family absorbed significantly less light than most loblolly pine families in the experiment, independent of cultural treatment, and families Lob 4 and Lob 5 had the highest APAR.

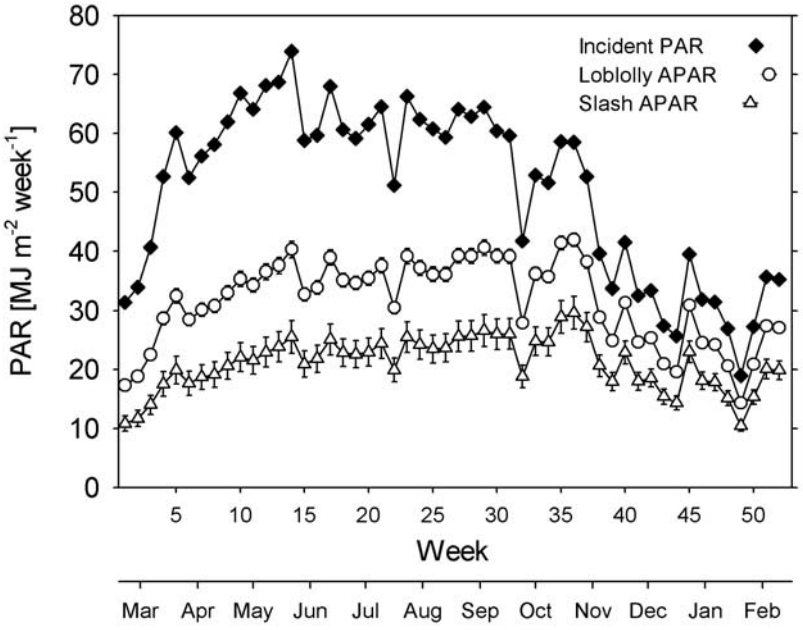

Figure 4.3. Weekly sums of incident PAR and APAR per ground area for two pine species at the DeRidder experimental site during the fourth growing season. Each open symbol represents a mean of 48 plots for loblolly pine and 8 plots for slash pine. Error bars indicate standard errors of the mean.

Similar to light absorption, the family effect on canopy net photosynthesis was significant in each month and for the entire year. The cultural treatment effect was not statistically significant, although values were higher by 14 to 36% in the HI than in the C treatment with the exception of the average-growing Lob 1 family (Table 4.3).

Table 4.3. Means (s.e.) of monthly sums and total annual sums of APAR and canopy net photosynthesis per unit ground area and light-use efficiency (ε) in loblolly and slash pine families under two contrasting silvicultural treatments during the fourth growing season (2005) at the DeRidder site.

	Monthly Total Absorbed PAR		**Annual Total Absorbed PAR**		**Monthly Total Canopy Net Photosynthesis**		**Annual Canopy Net Photosynthesis**		**ε**	
Family[1)]	[MJ m^{-2} $month^{-1}$]		[GJ m^{-2} $year^{-1}$]		[mol m^{-2} $month^{-1}$]		[mol m^{-2} $year^{-1}$]		[g MJ^{-1}]	
Lob 5	143.54	(5.33)	1.87^{a}	(0.10)	12.19	(0.48)	158.51^{a}	(10.36)	0.56^{a}	(0.03)
Lob 4	142.28	(5.49)	1.85^{a}	(0.13)	12.10	(0.49)	157.24^{a}	(12.18)	0.54^{ab}	(0.04)
Lob 2	123.27	(4.81)	1.60^{ab}	(0.12)	10.19	(0.43)	132.52^{ab}	(11.65)	0.44^{bc}	(0.02)
Lob 1	121.55	(4.45)	1.58^{ab}	(0.09)	10.12	(0.40)	131.60^{ab}	(9.37)	0.46^{abc}	(0.04)
Lob 3	121.26	(4.69)	1.58^{ab}	(0.11)	10.09	(0.42)	131.18^{ab}	(11.08)	0.41^{c}	(0.02)
Lob 7	105.73	(4.31)	1.37^{bc}	(0.12)	8.64	(0.39)	112.38^{b}	(11.55)	0.41^{c}	(0.02)
Slash 6	84.46	(3.54)	1.10^{c}	(0.11)	2.34	(0.11)	30.39^{c}	(3.75)	0.41^{c}	(0.02)
mean	**120.3**	**(1.9)**	**1.56**	**(0.05)**	**9.4**	**(0.2)**	**122.0**	**(6.6)**	**0.46**	**(0.01)**
Treatment[2)]										
C	110.7	(2.5)	1.44	(0.07)	8.5	(0.3)	110.5	(8.9)	0.46	(0.02)
HI	129.9	(2.8)	1.69	(0.07)	10.3	(0.3)	133.4	(9.3)	0.47	(0.02)

Source of Variation	**d.f.**	***P* > F**	***P* > F**	***P* > F**
treatment[3)]	1	0.1390	0.1186	0.7947
family	6	**<0.0001**	**<0.0001**	**0.0001**
fam x treatment	6	0.6113	0.4713	0.6759

[1)] Families are rank-ordered based on APAR. [2)] Silvicultural treatments as in Table 4.1; values followed with the same superscript letters are not significantly different for a given trait (family comparisons) at $\alpha = 0.05$ (Tukey-Kramer test). [3)]Block × cultural treatment with 3 d.f. was used as the error term for the treatment effect, and the residual error with 36 d.f. for the other effects.

When mid-season measurements of crown dimensions were included in the model (mid-season model), the simulated values of annual total APAR and net canopy photosynthesis varied by only 4 to 7% between the two modeling approaches (Table 4.4). The values were significantly different between the two models of crown growth for monthly values of APAR from May to September, and from May to August for canopy photosynthesis (data not shown).

Table 4.4. Comparison of means (s.e.) of annual sums of APAR and net canopy photosynthesis per unit ground area for two families of loblolly pine and one slash pine for linear and mid-season crown growth models.

		Annual Total Absorbed PAR		**Annual Canopy Net Photosynthesis**	
Family	Model	[MJ m^{-2} $year^{-1}$]		[mol m^{-2} $year^{-1}$]	
Lob 1	linear[1)]	1580.2	(91.2)	131.6	(9.4)
	mid-season	1693.6	(90.5)	140.2	(9.4)
Lob 5	linear	1866.0	(102.6)	158.5	(10.4)
	mid-season	1950.5	(97.8)	166.1	(10.1)
Slash 6	linear	1098.0	(108.8)	30.4	(3.8)
	mid-season	1168.9	(108.5)	31.8	(4.0)

[1)]The linear and mid-season models refer to linear crown growth between the beginning and the end of the annual simulation, and to the inclusion of the intermediate crown measurement, respectively; the model estimate differences (linear vs. mid-season) were not statistically significant. Each family mean is based on eight experimental plots.

4.4.4. Light-use efficiency

Light-use efficiency differed significantly among families and cultural treatment did not affect ε (Table 4.3). Within the range of observed LAI and APAR, ε varied from 0.28 to 0.68 g MJ^{-1}. In general, families that intercepted more light also had higher light-use efficiency (Table 4.3). Stand LAI, mean crown volume and canopy cover, when included together in a multiple regression analysis explained 72 and 88% of variation in ε in the C and HI treatment, respectively. However, most of this variation was explained by LAI (69 and 87%, respectively; Figure 4.4b). Although the overall effect of cultural treatment on ε was not statistically significant, the intercepts of the relationship between

ε and LAI differed between the two silvicultural treatments. At given LAI, light-use efficiency was on average 8% greater in the control than in the HI treatment (Figure 4.4b).

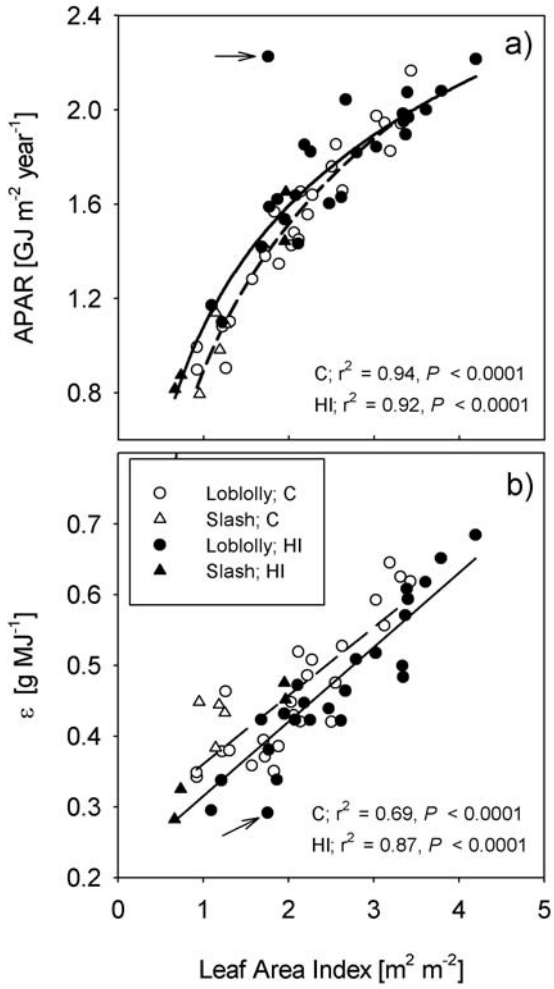

Figure 4.4. Relationship between leaf area index (LAI) and a) annual APAR, and b) light-use efficiency (ε) in loblolly and slash pine at the DeRidder site. Separate regressions were fit in a) for the C treatment $APAR = 0.895 + 0.895\ln(LAI)$ (dashed line), and HI treatment $APAR = 1.081 + 0.74\ln(LAI)$ (solid line), and in b) for the C treatment $\varepsilon = 0.26 + 0.097LAI$ (dashed line) and for HI treatment $\varepsilon = 0.21 + 0.10\ LAI$ (solid line). Each point represents an individual plot; the outlier indicated by an arrow was excluded from the analysis.

The relationship between aboveground biomass increment and APAR was non-linear across species and families (Figure 4.5a). This non-linearity was observed because APAR was an exponential function of LAI (Figure 4.4a), whereas the relationship between aboveground growth and LAI was linear (Figure 4.5b). In addition, the intercept of the aboveground biomass increment and APAR relationship was higher in the control than HI treatment.

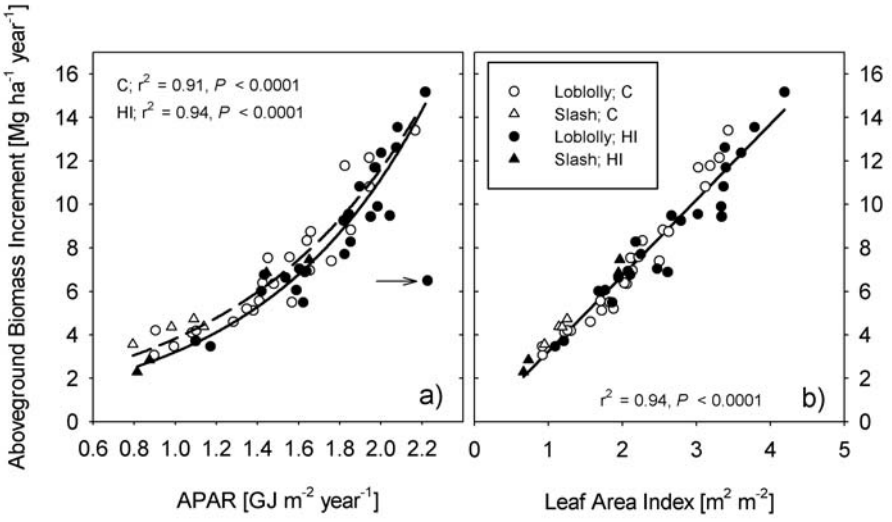

Figure 4.5. Relationship between annual aboveground biomass (ABI) increment and a) APAR and b) leaf area index (LAI) for loblolly and slash pine families during the fourth growing season. Separate regressions were fit in a) for the HI treatment: $\ln(ABI) = -0.08 + 0.0012\ APAR$, n = 27 (solid line, closed symbols), and for the C treatment: $\ln(ABI) = 0.29 + 0.0011\ APAR$, n = 28 (dashed line, open symbols). A single regression line across families and treatments was fit in b) $ABI = -0.24 + 3.48\ LAI$, n = 56. Each point represents an individual plot; the outlier indicated by an arrow was excluded from the analysis.

Total annual aboveground biomass increment was related to canopy photosynthesis (Figure 4.6). Although families within loblolly pine differed in the intercepts of the relationship (data not shown), species differences were larger. The relationship of aboveground biomass increment with total photosynthesis was non-linear for loblolly pine and differed from that of the slash pine family (Figure 4.6).

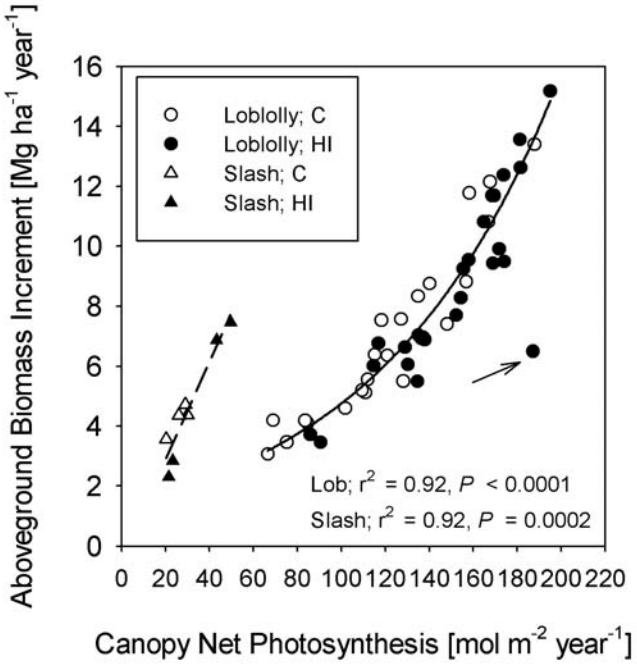

Figure 4.6. Relationship between annual aboveground biomass increment (ABI) and simulated annual canopy photosynthesis (Ps) per unit ground area in loblolly and slash pine families at the DeRidder site. Regression fits are $\ln(ABI) = 0.39 + 0.012Ps$, solid line, n = 47 for loblolly pine, and $ABI = -0.41 + 0.16Ps$, n = 8, for slash pine. The outlier indicated by an arrow was excluded from the analysis.

4.5. Discussion

Using the process-based model MAESTRA, we simulated canopy light interception and photosynthesis in young stands of loblolly and slash pine approaching canopy closure, and related these estimates with observed differences in aboveground productivity. The range of values of standing stem-wood biomass and aboveground biomass, and their current annual increments observed in our stands were well within the range for loblolly and slash pine receiving fertilization at similar ages and stand stocking (Colbert et al., 1990; Dalla-Tea and Jokela, 1991; McCrady and Jokela, 1998; Will et al., 2002; Burkes et al., 2003). For the most productive loblolly pine family (Lob 5) and

slash pine family (Slash 6), the growth estimates were higher compared to literature results (Colbert et al., 1990).

Family and species effects were most pronounced in growth and crown traits in our study, whereas the effect of silvicultural treatment was not statistically significant. Although family differences in productivity and crown structure were reported for loblolly pine (Dalla-Tea and Jokela, 1991; McCrady and Jokela, 1996; 1998; Chmura et al., 2007; Emhart et al., 2007), the lack of a significant growth response to nutrient additions and control of competing vegetation is perhaps in contrast with many other studies in southern pines (Jokela et al., 2004 and associated studies). However, growth, crown size and leaf area were generally greater in the HI than in control treatment in our experiment. It should be noted that our "control" treatment received fertilization and vegetation control at the time of planting, which may partially mute the differences expected between silvicultural treatments, if native soil fertility was used as the C treatment.

The mean estimates of light-use efficiency obtained in our study were within the range reported for other pine species (Stenberg et al., 1994). The values for slash pine family in our experiment corresponded very well with values reported in Dalla-Tea and Jokela (1991), but ε of our loblolly pine families were lower than in other studies at a similar age (Dalla-Tea and Jokela, 1991; McCrady and Jokela, 1998). However, in the study by McCrady and Jokela (1998), stand density was different than in our experiment, precluding a direct comparison. Our measured values of light interception agreed very well with APAR simulated by the model; therefore, we conclude that the MAESTRA model provided reliable estimates of APAR in our pine stands. It should be noted, however, that simulated estimates of APAR and canopy photosynthesis have no measurement error, and the error term estimates (Tables 4.3 and 4.4) represent plot-to-plot variation in the input variables.

Families Lob 4 and Lob 5 not only absorbed more light than other genotypes in the experiment, but also had the greatest ε. Light-use efficiency was the lowest for the slash pine family, which seems to confirm the species contrast presented in Dalla-Tea

and Jokela (1991); however, species differences in ε were not statistically significant in our study (see Table 4.3). Likewise, silvicultural treatment had no significant effect on light-use efficiency in our study, suggesting that this trait may be relatively stable in genotypes. Persistent family differences in ε might be useful in estimation of productivity in intensively managed pine plantations, provided reliable estimates of light absorption were available. However, Gholz et al. (1991) argued that light-use efficiency for slash pine stands might vary both from year-to-year and seasonally, as a result of fluctuations in canopy leaf area. Further research is needed to resolve this point.

In contrast to other empirical and modeling studies reporting linear or near-linear relationships between intercepted light and annual aboveground biomass production (Cannell, 1989; McMurtrie et al., 1992; Medlyn, 1998; Will et al., 2001; Will et al., 2005), we found a non-linear relationship, suggesting increasing light-use efficiency at higher levels of APAR. Although canopy closure had begun in our stands at the time of study, not all plots had closed stands, and thus exhibited a range in LAI values. Consequently, among-family variation in LAI (82%) and APAR (52%) was more responsible for observed variation in aboveground growth (80%) than differences in ε (33%) alone, although these traits together are important determinants of productivity. The effects of family or species differences in light-use efficiency would be expected to be further amplified in fully stocked stands at peak LAI and APAR (Green et al., 2001).

The examined families differed in crown size, accumulated leaf area and canopy cover, which had distinct effects on canopy light interception. Loblolly pine families with the largest crowns and highest leaf area index intercepted more light and grew more than families with smaller crowns. Moreover, all experimental plots shared a single relationship of LAI and aboveground growth, with no apparent species or cultural treatment differences. However, light absorption was a non-linear function of leaf area and differed between two cultural treatments. At given LAI, plots in the C treatment absorbed less PAR than plots in the HI treatment – the effect of generally smaller, denser crowns, resulting in more self-shading in the C than in the HI treatment.

It is possible that trees in the two cultural treatments also differed in relative allocation of biomass belowground. We did not examine belowground allocation in the current study; however, relative allocation of biomass to taproot and coarse roots did not differ between families and treatments at age 2 years (D.J. Chmura, unpublished results). Moreover, if trees in the control treatment were nutrient-limited, we would rather observe increased allocation belowground (Gower et al., 1994; Samuelson, 2000), and consequently lower light-use efficiency based on aboveground biomass than in the HI treatment. Thus, although differences in crown attributes between cultural treatments may explain differences in light absorption at similar LAI, the exact cause of differences in light-use efficiency at the same stand leaf area remains obscure. However, the overall effect of cultural treatment on both APAR and light-use efficiency was small, and most variability was associated with family and species differences. The slash pine family had the greatest leaf area density among the examined families, which confirmed our observation from these same stands at age 2 years (Chmura et al., 2007). At age 2 years, we found family differences in crown shape (Chmura et al., 2007), but these differences had largely disappeared by age 4 years, perhaps as a result of crown closure and recession. However, at canopy closure, crown shape itself might be of minor importance for canopy light interception (Wang and Jarvis, 1990b) compared to other crown attributes, such as total leaf area and crown size.

Vertical leaf area distribution in our trees was similar in both species for both current and previous year foliage age cohorts. Silvicultural treatment had little effect on vertical leaf area distribution in our study. This finding is in agreement with Gillespie et al. (1994) for leaf biomass distribution in loblolly pine, although actual leaf area distribution in that study may differ due to variation in SLA within crowns (Adams et al., 1986; Meir et al., 2002; McGarvey et al., 2004; Chmura and Tjoelker, *in press*). Vose (1988) also reported no change in vertical LAI distribution in fertilized loblolly pine stands, but the effect was dependent on the initial LAI of a stand. Within a stand with higher LAI, more leaf area was distributed in the upper canopy. In contrast, Wang et al. (1990) showed downward shifts of leaf area distribution in both current and 1-year-

old foliage of irrigated and fertilized radiata pine (*Pinus radiata* D. Don.) stands compared to the control.

Although the relationship of photosynthesis with intercepted light is non-linear, integration across longer time periods, such as a growing season, tends to linearize the relationship (Stenberg et al., 1994; Sands, 1996; Medlyn et al., 2003). Despite a lack of differences in instantaneous, light-saturated leaf-level rates of net photosynthesis (Chmura and Tjoelker, *in press*), estimates of total annual carbon gain at the canopy scale differed among the tested families in our study. In addition, we found a positive relationship between aboveground growth and canopy photosynthesis, and no such relationship with physiological attributes at the leaf level (Chmura and Tjoelker, *in press*). These findings suggest that instantaneous physiological parameters may not be as informative as integrated canopy-scale estimates in relating physiological properties with stand productivity. Our results indicate that slash pine had greater aboveground growth per given canopy photosynthesis than loblolly pine. This relationship reflects species differences in the leaf photosynthetic parameters used in our simulations (see Table C.1), although we are not able to rule-out higher efficiency of incorporating assimilates into biomass in slash than in loblolly pine. Nonetheless, the lower productivity of slash pine compared to loblolly pine suggests that other canopy characteristics, such as a lower total leaf area and increased packing of foliage within the crown volume, and allocation patterns were likely the cause of its lower aboveground production.

The MAESTRA model gave similar results whether or not a mid-season correction of crown growth was used in an annual simulation. However, estimates differed between the two modeling scenarios during months when both APAR and canopy photosynthesis were the highest. Thus, differences between linear and mid-season crown growth models were magnified at some points during the growing season, but were muted when integrated at annual scale. To avoid potential compounding of error throughout longer time periods, we suggest that canopy size metrics as detailed as possible should be used throughout the course of the simulation period. In general, the model might be useful for estimation of stand APAR and derivation of light-use

efficiency in the practice of forestry. However, the model requires a number of parameters that are not usually measured during inventories (e.g. crown metrics) or readily available. Whereas leaf-level physiological parameters might be found in the literature for numerous species, others, such as parameters for leaf area distribution are rarely published. Moreover, some of these parameters might be specific to species, genotype, age, stand stocking and nutrition. Our data and the results from other studies in pines (Vose, 1988; Gillespie et al., 1994) suggest that species differences associated with LAI were more important in comparisons of productivity than the effects of family or silvicultural treatment on vertical leaf area distribution. However, the utility of the model will perhaps remain in experimental settings, unless more stand parameters are measured in the field.

In summary, we found pronounced differences in aboveground growth and canopy light absorption and photosynthesis among selected families of loblolly and slash pine at the onset of canopy closure. Aboveground biomass productivity was positively but non-linearly related to APAR and canopy photosynthesis, and light-use efficiency varied among families, with slash pine having the lowest ε. Based on our study we are not able to identify the exact causes of increased light-use efficiency, but it is possible to identify attributes of the most productive genotypes. Light absorption was related to total leaf area and its distribution within the crown. Families with more leaf area, larger crowns, thus with low leaf area density and with crowns effectively occupying the growing space absorbed the most light and grew the most. Silvicultural treatment effects on growth and light absorption parameters were not statistically significant in our study, although tree growth, crown size, leaf area, and light absorption were generally greater in the treatment receiving fertilization and vegetation control than in the control treatment. Intensive silvicultural treatment had little effect on the vertical leaf area distribution in loblolly and slash pine. These findings may be useful in modeling productivity in intensively managed pine plantations.

5. SUMMARY

Crown architecture and size affects tree growth through control of leaf area and its display for light capture and photosynthesis. It is important to quantify crown and canopy traits for effective use of intensive silvicultural practices to improve tree growth in forest plantations. This dissertation addresses the linkages between crown structure, within-crown leaf morphology and physiology and aboveground growth in one slash pine family and six selected families of loblolly pine, differing in growth rate. Two contrasting silvicultural treatments comprised of repeated fertilization with control of competing vegetation (HI), and a control (C) that included fertilization and weed control at planting, were applied at three experimental sites in the West Gulf Coastal Plain of Texas and Louisiana. Tree growth was measured throughout the first six years of stand development.

5.1. Growth and Biomass Allocation in Relation to Crown Structure in Young Stands

Before canopy closure at age 2 years, differences in aboveground growth among all seven families were significant. Family rankings and the strength of effect of silvicultural treatments differed among experimental sites. Although the HI treatment increased aboveground growth compared to the control at all three sites, the only significant response at an early stand age was observed at the most productive site in Kirbyville, TX. The site differences might be associated with variation in soil drainage class, as mean productivity declined with decreasing soil drainage among sites.

Three sampled families differed in allocation patterns, with slash pine allocating proportionately more aboveground biomass in stemwood and less in branches than the two loblolly pine families (Section 2). When variation in tree size was accounted for, loblolly pine families produced significantly larger crowns than slash pine. The most productive family, Lob 5, had the greatest aboveground leaf area ratio and a different crown shape than the two other genotypes. However, when compared at the same crown

volume, slash pine maintained a comparable leaf area as that of loblolly pine and produced more stemwood biomass. Thus slash pine had greater leaf area density per crown volume than loblolly pine, and family differences in leaf area ratio were controlled more by variation in leaf mass fraction than in specific leaf area. Growth efficiency (ratio of stemwood growth to leaf area) was similar in both species; therefore, the larger leaf area per crown volume in slash pine compensated for its smaller crowns compared to loblolly pine in terms of aboveground growth at an early age. Across all families, accumulation of aboveground biomass was related to crown volume, but relative allocation to aboveground components was independent of crown traits. Silvicultural treatment had no statistically significant effects on crown traits and aboveground biomass allocation patterns. These findings suggest that crown shape might be important for leaf area distribution, light capture and canopy carbon gain prior to canopy closure. However, the results point to the importance of crown size and accumulated leaf area in aboveground productivity among the examined pine families.

5.2. Gradients of Leaf Morphological and Physiological Attributes Related to Light Availability Within Crowns

Canopy closure began during the fourth and fifth growing seasons, as crowns approached their maximum diameters and began to recede - changes typical to this stage of stand development (Section 3). At that time, steep gradients of leaf morphology (SLA) and foliar nitrogen (N) had developed. SLA increased and leaf N concentrations decreased with crown depth in both species, although slash pine had significantly lower SLA and mass-based foliar N concentrations than loblolly pine in all crown positions. Within-crown gradients of these traits were generally steeper in loblolly pine families than in slash pine. Light-saturated photosynthetic rates in leaves decreased from upper to lower canopy when expressed on a leaf-area basis, and the two pine species did not differ in leaf-level photosynthesis. Observed changes in leaf traits resulted from expected acclimation to developing light availability gradients within closing canopies

(Field, 1983; Hollinger, 1996; Niinemets et al., 1998). Leaf photosynthesis was positively correlated with leaf nitrogen, but depended upon site and cultural treatment. Overall, the effect of silvicultural treatment on within-crown gradients of leaf morphology, chemistry and physiology was not significant, except for leaf N and chlorophyll concentrations at one of the sites (Kirbyville, Texas). Aboveground growth was not directly related to leaf-level photosynthetic rates, but was related to the fraction of intercepted PAR at the canopy level.

5.3. Aboveground Productivity in Relation to Canopy Traits that Affect Light Absorption and Photosynthesis

Simulations with the process-based model MAESTRA supported the importance of accumulated leaf area and crown size for light interception and canopy photosynthesis. At the onset of canopy closure, families with larger crowns, higher leaf area index (LAI) and greater canopy cover absorbed the most light and grew the most (Section 4). Silvicultural treatment effects on growth, leaf area distribution and light absorption parameters were not statistically significant, although tree growth, crown size, leaf area, and light absorption were generally greater in the high intensity treatment than in the control treatment. The general lack of statistical significance of differences between the two silvicultural treatments in tree growth and leaf area was in contrast to other studies in the two pine species (Colbert et al., 1990; Martin and Jokela, 2004b), but was likely a result of the fertilization and weed control that both treatments received at the time of site preparation. Trees in the control treatment likely did not develop nutrient limitations or deficiency, at least in terms of nitrogen supply, as the foliar concentrations were generally higher than critical levels for the two pine species. Phosphorus limitation was not present at age 2 years; however, this nutrient is often limiting productivity in pine stands throughout the Southeastern United States (Allen et al., 1990).

Examination of time-integrated water-use efficiency using stable carbon isotope methods did not provide conclusive findings linking aboveground growth to either

increased or decreased water-use efficiency in our experiment, although families differed in this trait (Appendix B). Leaf-level physiology was not directly correlated with aboveground productivity, but did provide an insight into differences among the examined families. In contrast to instantaneous leaf-level photosynthetic rates, the correlation of aboveground productivity with estimates of canopy photosynthesis was strong and positive. Thus, integration from leaf to canopy scale that incorporates the above-mentioned suite of crown and canopy traits governing light-capture and canopy carbon gain provides a link between aboveground growth and physiological properties in forest stands.

5.4. Implications for Genotype Selection and Plantation Forestry

The presented results provide partial support for the hypothesis of greater productivity of families with a more plastic response of leaf traits to within-crown light gradients. Slash pine had the lowest aboveground growth and not as steep gradients in leaf traits within crowns in comparison to the loblolly pine families. However, other traits, such as overall leaf area and its distribution within the crown volume might be of equal or greater importance for canopy light capture and photosynthesis. Moreover, families differed in light-use efficiency (ε). It is likely that differences in the efficiency of incorporating assimilated carbon into biomass and allocation differences play a role in among-family variation in light-use efficiency. However, the exact causes and effects of family differences in light-use efficiency require further investigation. Aboveground biomass increment and APAR, and thus light-use efficiency were each strongly related to stand leaf area index. The strong functional relationship between LAI and annual biomass increment confirms similar relationships reported in other studies of loblolly and slash pine (Albaugh et al., 2004; Borders et al., 2004; Martin and Jokela, 2004a; Samuelson et al., 2004). Given that, it may be possible to use remotely-sensed LAI (Running et al., 1986; Peterson et al., 1987; Curran et al., 1992; Flores et al., 2006) to model aboveground productivity in southern pine plantations.

Presented results indicate that linking morphology and physiology with aboveground productivity in our pine stands requires integration of traits from individual leaves to crowns and canopies. Family differentiation it tree growth and stand productivity was generally greater when canopy attributes were examined, compared to leaf-level characteristics. A suite of morphological traits associated with productive genotypes might be identified that should help in guiding the selection criteria for the most productive ideotypes among genotypes of southern pines (Dickmann, 1985; Martin et al., 2001). The most productive family (Lob 5) had the largest crowns, a high leaf area index and the lowest leaf area density. Consequently, this family likely exhibited the least amount of self-shading and had the highest canopy cover, thus effectively intercepted solar radiation at the stand level. In addition, this family exhibited some of the physiological attributes of a crop ideotype - highest light- and water-use efficiency; yet, its photosynthetic nitrogen-use efficiency was the lowest. Thus, increased crown size and low leaf area density show promise as potential selection criteria for productive genotypes. In contrast, the least productive family (Slash 6) had nearly the opposite suite of traits. However, these findings do not preclude planting slash pine in intensively managed plantations on suitable sites. Greater allocation of aboveground biomass into stem in slash than in loblolly pine found in our study, may make slash pine a better choice for plantation forestry, depending on production goals. Competitive interactions might change with stand development and will depend on deployment strategies. It is conceivable that genotypes approaching a crop ideotype in pure family plots might demonstrate a contrasting competitive ideotype when deployed in mixed family plantations.

REFERENCES

Adams, M. B., Allen, H. L., Davey, C. B., 1986. Accumulation of starch in roots and foliage of loblolly pine (*Pinus taeda* L.): Effects of season, site and fertilization. Tree Physiol. 2, 35-46.

Albaugh, T. J., Allen, H. L., Dougherty, P. M., Kress, L. W., King, J. S., 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. 44, 317-328.

Albaugh, T. J., Lee Allen, H., Dougherty, P. M., Johnsen, K. H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. For. Ecol. Manage. 192, 3-19.

Allen, H. L., Dougherty, P. M., Campbell, R. G., 1990. Manipulation of water and nutrients - Practice and opportunity in Southern U.S. pine forests. For. Ecol. Manage. 30, 437-453.

Allen, H. L., Fox, T. R., Campbell, R. G., 2005. What is ahead for intensive pine plantation silviculture in the south? South. J. Appl. For. 29, 62-69.

Baldocchi, D. D., Hicks, B. B., Meyers, T. P., 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology. 69, 1331-1340.

Baldwin, V. C., Burkhart, H. E., Dougherty, P. M., Teskey, R. O., 1993. Using a growth and yield model (Ptaeda2) as a driver for a biological process model (MAESTRO). USDA For. Serv. South. For. Exp. Stn. Res. Pap. 276, 1-9.

Baldwin, V. C., Peterson, K. D., 1997. Predicting the crown shape of loblolly pine trees. Can. J. For. Res. 27, 102-107.

Baldwin, V. C., Dougherty, P. M., Burkhard, H. E., 1998. Linked model for simulating stand development and growth processes of loblolly pine. In: Mickler, R. A., Fox, S. (Eds.), The Productivity and Sustainability of Southern Forest Ecosystems in a

Changing Environment. Ecological Studies 128. Springer-Verlag, New York, pp. 305-325.

Blazier, M. A., Hennessey, T. C., Lynch, T. B., Wittwer, R. F., Payton, M. E., 2004. Productivity, crown architecture, and gas exchange of North Carolina and Oklahoma/Arkansas loblolly pine families growing on a droughty site in southeastern Oklahoma. For. Ecol. Manage. 194, 83-94.

Bond, B. J., Farnsworth, B. T., Coulombe, R. A., Winner, W. E., 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. Oecologia. 120, 183-192.

Boote, K. J., Loomis, R. S., 1991. The prediction of canopy assimilation. In: Boote, K. J., Loomis, R. S. (Eds.), Modeling Crop Photosynthesis - From Biochemistry to Canopy. Crop Science Society of America, Inc., American Society of Agronomy, Inc., Madison, Wisconsin, pp. 109-140.

Borders, B. E., Will, R. E., Markewitz, D., Clark, A., Hendrick, R., Teskey, R. O., Zhang, Y., 2004. Effect of complete competition control and annual fertilization on stem growth and canopy relations for a chronosequence of loblolly pine plantations in the lower coastal plain of Georgia. For. Ecol. Manage. 192, 21-37.

Burkes, E. C., Will, R. E., Barron-Gafford, G. A., Teskey, R. O., Shiver, B., 2003. Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliottii* stands of different planting densities For. Sci. 49, 224-234.

Cannell, M. G. R., 1989. Light interception, light use efficiency and assimilate partitioning in poplar and willow stands. In: Pereira, J. S., Landsberg, J. J. (Eds.), Biomass Production by Fast-growing Trees. Kluwer Academic Publishers, Dordrecht, pp. 1-12.

Chapin, F. S., Matson, P. A., Mooney, H. A., 2002. Principles in Terrestrial Plant Ecology. Springer, New York, pp. 436.

Chmura, D. J., Rahman, M. S., Tjoelker, M. G., 2007. Crown structure and biomass allocation patterns modulate aboveground productivity in young loblolly pine and slash pine. For. Ecol. Manage. 243, 219-230.

Chmura, D. J., Tjoelker, M. G., 2008. Leaf traits in relation to crown development, light interception, and growth of elite families of loblolly and slash pine. Tree Physiol. *in press.*

Colbert, S. R., Jokela, E. J., Neary, D. G., 1990. Effects of annual fertilization and sustained weed control on dry-matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. For. Sci. 36, 995-1014.

Cornelissen, J. H. C., Castro-Diez, P., Carnelli, A. L., 1998. Variation in relative growth rate among woody species. In: Lambers, H., Poorter, H., Van Vuuren, M. M. I. (Eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, The Netherlands, pp. 363-392.

Cropper, W. P., Gholz, H. L., 1993. Simulation of the carbon dynamics of a Florida slash pine plantation. Ecol. Model. 66, 231-249.

Cropper, W. P. J., Peterson, K., Teskey, R. O., 1998. MAESTRO simulations of the response of loblolly pine to elevated temperatures and carbon dioxide. In: Mickler, R. A., Fox, S. (Eds.), The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment. Ecological Studies 128. Springer-Verlag, New York, pp. 327-339.

Crous, K. Y., Ellsworth, D. S., 2004. Canopy position affects photosynthetic adjustments to long-term elevated CO2 concentration (FACE) in aging needles in a mature *Pinus taeda* forest. Tree Physiol. 24, 961-970.

Curran, P. J., Dungan, J. L., Gholz, H. L., 1992. Seasonal LAI in slash pine estimated with Landsat TM. Remote Sens. Environ. 39, 3-13.

Dalla-Tea, F., Jokela, E. J., 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. For. Sci. 37, 1298-1313.

De Pury, D. G. G., Farquhar, G. D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ. 20, 537-557.

DeLucia, E. H., Schlesinger, W. H., 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. Ecology. 72, 51-58.

Dewar, R. C., 1996. The correlation between plant growth and intercepted radiation: An interpretation in terms of optimal plant nitrogen content. Ann. Bot. 78, 125-136.

Dickmann, D. I., 1985. The ideotype concept applied to forest trees. In: Cannell, M. G. R., Jackson, J. E. (Eds.), Attributes of Trees as Crop Plants. Insititute of Terrestrial Ecology Huntington, England, pp. 89 - 101.

Dudley, S. A., 1996. Differing selection on plant physiological traits in response to environmental water availability: A test of adaptive hypotheses. Evolution. 50, 92-102.

Ellsworth, D. S., Reich, P. B., 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia. 96, 169-178.

Elmore, C. D., 1980. The paradox of no correlation between leaf photosynthetic rates and crop yields. In: Hesketh, J. D., Jones, J. W. (Eds.), Predicting Photosynthesis for Ecosystem Models. Vol. II. CRC Press Inc., Boca Raton, Florida, pp. 155-167.

Emhart, V. I., Martin, T. A., White, T. L., Huber, D. A., 2007. Clonal variation in crown structure, absorbed photosynthetically active radiation and growth of loblolly pine and slash pine. Tree Physiol. 27, 421-430.

Evans, J. R., Farquhar, G. D., 1991. Modeling canopy photosynthesis from biochemistry of the C_3 chloroplast. In: Boote, K. J., Loomis, R. S. (Eds.), Modeling Crop Photosynthesis - From Biochemistry to Canopy. Crop Science Society of America, Inc., American Society of Agronomy, Inc., Madison, Wisconsin, pp. 1-15.

Farquhar, G. D., von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O. L., Nobel, P. S., Osmond, C. B., Ziegler, H. (Eds.), Physiological Plant Ecology II. Water Relations and Carbon Assimilation. Springer-Verlag, Berlin, Heidelberg, pp. 549-587.

Field, C., 1983. Allocating leaf nitrogen for the maximization of carbon gain - leaf age as a control on the allocation program. Oecologia. 56, 341-347.

Field, C., Merino, J., Mooney, H. A., 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia. 60, 384-389.

Flores, F. J., Allen, H. L., Cheshire, H. M., Davis, J. M., Fuentes, M., Kelting, D., 2006. Using multispectral satellite imagery to estimate leaf area and response to silvicultural treatments in loblolly pine stands. Can. J. For. Res. 36, 1587-1596.

Gay, L. W., Knoerr, K. R., Braaten, M. O., 1971. Solar radiation variability on floor of a pine plantation. Agric. Meteorol. 8, 39-50.

Gholz, H. L., Fisher, R. F., 1982. Organic matter production and distribution in slash pine (*Pinus elliottii*) plantations. Ecology. 63, 1827-1839.

Gholz, H. L., Vogel, S. A., Cropper, W. P., McKelvey, K., Ewel, K. C., Teskey, R. O., Curran, P. J., 1991. Dynamics of canopy structure and light interception in *Pinus elliottii* stands, North Florida. Ecol. Monogr. 61, 33-51.

Gillespie, A. R., Allen, H. L., Vose, J. M., 1994. Amount and vertical distribution of foliage of young loblolly pine trees as affected by canopy position and silvicultural treatment. Can. J. For. Res. 24, 1337-1344.

Gough, C. M., Seiler, J. R., Maier, C. A., 2004a. Short-term effects of fertilization on loblolly pine (*Pinus taeda* L.) physiology. Plant, Cell and Environment. 27, 876-886.

Gough, C. M., Seiler, J. R., Johnsen, K. H., Sampson, D. A., 2004b. Seasonal photosynthesis in fertilized and nonfertilized loblolly pine. For. Sci. 50, 1-9.

Gower, S. T., Gholz, H. L., Nakane, K., Baldwin, V. C., 1994. Production and carbon allocation patterns of pine forests. In: Gholz, H. L., Linder, S., McMurtrie, R. E. (Eds.), Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Ecol. Bull., Copenhagen, 43, pp. 115-135.

Gravatt, D. A., Chambers, J. L., Barnett, J. P., 1997. Temporal and spatial patterns of net photosynthesis in 12-year-old loblolly pine five growing seasons after thinning. For. Ecol. Manage. 97, 73-83.

Green, D. S., Kruger, E. L., Stanosz, G. R., Isebrands, J. G., 2001. Light-use efficiency of native and hybrid poplar genotypes at high levels of intracanopy competition. Can. J. For. Res. 31, 1030-1037.

Gregoire, N., Fisher, R. F., 2004. Nutritional diagnoses in loblolly pine (*Pinus taeda* L.) established stands using three different approaches. For. Ecol. Manage. 203, 195-208.

Griffiths, H., 1991. Applications of stable isotope technology in physiological ecology. Funct. Ecol. 5, 254-269.

Haissig, B. E., Dickson, R. E., 1979. Starch measurement in plant tissue using enzymatic hydrolysis. Physiol. Plant. 47, 151-157.

Haxeltine, A., Prentice, I. C., 1996. A general model for the light-use efficiency of primary production. Funct. Ecol. 10, 551-561.

Hirose, T., Werger, M. J. A., 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia. 72, 520-526.

Hollinger, D. Y., 1996. Optimality and nitrogen allocation in a tree canopy. Tree Physiol. 16, 627 - 634.

Ibrom, A., Jarvis, P. G., Clement, R., Morgenstern, K., Oltchev, A., Medlyn, B. E., Wang, Y. P., Wingate, L., Moncrieff, J. B., Gravenhorst, G., 2006. A comparative analysis of simulated and observed photosynthetic CO_2 uptake in two coniferous forest canopies. Tree Physiol. 26, 845-864.

Iio, A., Fukasawa, H., Nose, Y., Kato, S., Kakubari, Y., 2005. Vertical, horizontal and azimuthal variations in leaf photosynthetic characteristics within a *Fagus crenata* crown in relation to light acclimation. Tree Physiol. 25, 533-544.

Jarvis, P. G., 1995. Scaling processes and problems. Plant Cell Environ. 18, 1079-1089.

Johnson, J. D., 1984. A rapid technique for estimating total surface area of pine needles. For. Sci. 30, 913-921.

Jokela, E. J., Wilson, D. S., Allen, J. E., 2000. Early growth responses of slash and loblolly pine following fertilization and herbaceous weed control treatments at establishment. South. J. Appl. For. 24, 23-30.

Jokela, E. J., Martin, T. A., 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Can. J. For. Res. 30, 1511-1524.

Jokela, E. J., Dougherty, P. M., Martin, T. A., 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: A synthesis of seven long-term experiments. For. Ecol. Manage. 192, 117-130.

Jokela, E. J., 2002. Nutrient management of Southern pines. In: Dickens, E. D., Barnett, J. P., Hubbard, W. G., Jokela, E. J. (Eds.), Slash Pine: Still Growing and Growing! Proceedings of the Slash Pine Symposium, Jekyll Island, Georgia, April 23–25, 2002. USDA For. Serv. Gen. Tech. Rep. SRS-76, Asheville, NC, pp. 27-35.

Kimmins, J. P., 1997. Forest Ecology. A Foundation for Sustainable Management. Prentice Hall, Upper Saddle River, New Jersey, pp. 596.

Kruger, E. L., Volin, J. C., 2006. Reexamining the empirical relation between plant growth and leaf photosynthesis. Funct. Plant Biol. 33, 421-429.

Kuuluvainen, T., Pukkala, T., 1989. Simulation of within-tree and between-tree shading of direct radiation in a forest canopy: Effect of crown shape and sun elevation. Ecol. Model. 49, 89-100.

Lambers, H., Chapin, F. S., Pons, T. L., 1998. Plant Physiological Ecology. Springer-Verlag, New York, pp. 450.

Livingston, N. J., Whitehead, D., Kelliher, F. M., Wang, Y. P., Grace, J. C., Walcroft, A. S., Byers, J. N., McSeveny, T. M., Millard, P., 1998. Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young *Pinus radiata* D. Don tree. Plant Cell Environ. 21, 795-803.

Lopez-Upton, J., White, T. L., Huber, D. A., 2000. Species differences in early growth and rust incidence of loblolly and slash pine. For. Ecol. Manage. 132, 211-222.

Luo, Y., Medlyn, B., Hui, D., Ellsworth, D., Reynolds, J., Katul, G., 2001. Gross primary productivity in Duke Forest: Modeling synthesis of CO_2 experiment and eddy-flux data. Ecol. Appl. 11, 239-252.

Maguire, D. A., Bennett, W. S., 1996. Patterns in vertical distribution of foliage in young coastal Douglas-fir. Can. J. For. Res. 26, 1991-2005.

Maier, C. A., Johnsen, K. H., Butnor, J., Kress, L. W., Anderson, P. H., 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees in response to elevated carbon dioxide concentration and fertilization. Tree Physiol. 22, 1093-1106.

Martin, T. A., Johnsen, K. H., White, T. L., 2001. Ideotype development in southern pines: Rationale and strategies for overcoming scale-related obstacles. For. Sci. 47, 21-28.

Martin, T. A., Jokela, E. J., 2004a. Stand development and production dynamics of loblolly pine under a range of cultural treatments in north-central Florida USA. For. Ecol. Manage. 192, 39-58.

Martin, T. A., Jokela, E. J., 2004b. Developmental patterns and nutrition impact radiation use efficiency components in southern pine stands. Ecol. Appl. 14, 1839-1854.

Martin, T. A., Dougherty, P. M., McKeand, S. E., 2005. Strategies and case studies for incorporating ecophysiology into southern pine tree improvement programs. South. J. Appl. For. 29, 70-79.

McCartney, H. A., 1978. Spectral distribution of solar radiation. II. Global and diffuse. Q. J. R. Meteorol. Soc. 104, 911-926.

McCrady, R. L., Jokela, E. J., 1996. Growth phenology and crown structure of selected loblolly pine families planted at two spacings. For. Sci. 42, 46-57.

McCrady, R. L., Jokela, E. J., 1998. Canopy dynamics, light interception, and radiation use efficiency of selected loblolly pine families. For. Sci. 44, 64-72.

McGarvey, R. C., Martin, T. A., White, T. L., 2004. Integrating within-crown variation in net photosynthesis in loblolly and slash pine families. Tree Physiol. 24, 1209-1220.

McKeand, S., Mullin, T., Byram, T., White, T., 2003. Deployment of genetically improved loblolly and slash pines in the south. J. For. 101, 32-37.

McKeand, S. E., Jokela, E. J., Huber, D. A., Byram, T. D., Allen, H. L., Li, B. L., Mullin, T. J., 2006. Performance of improved genotypes of loblolly pine across different soils, climates, and silvicultural inputs. For. Ecol. Manage. 227, 178-184.

McMurtrie, R. E., Leuning, R., Thompson, W. A., Wheeler, A. M., 1992. A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf CO_2 exchange. For. Ecol. Manage. 52, 261-278.

McMurtrie, R. E., Gholz, H. L., Linder, S., Gower, S. T., 1994. Climatic factors controlling productivity of pine stands: a model-based analysis. In: Gholz, H. L., Linder, S., McMurtrie, R. E. (Eds.), Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Ecol. Bull., Copenhagen, 43, pp. 173-188.

Medlyn, B., Barrett, D., Landsberg, J., Sands, P., Clement, R., 2003. Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. Funct. Plant Biol. 30, 153-169.

Medlyn, B. E., 1998. Physiological basis of the light use efficiency model. Tree Physiol. 18, 167-176.

Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A., Jarvis, P. G., 2002. Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. Plant Cell Environ. 25, 343-357.

Monteith, J. L., 1977. Climate and efficiency of crop production in Britain. Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci. 281, 277-294.

Munger, G. T., Will, R. E., Borders, B. E., 2003. Effects of competition control and annual nitrogen fertilization on gas exchange of different-aged *Pinus taeda*. Can. J. For. Res. 33, 1076-1083.

Murthy, R., Dougherty, P. M., Zarnoch, S. J., Allen, H. L., 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. Tree Physiol. 16, 537-546.

Murthy, R., Zarnoch, S. J., Dougherty, P. M., 1997. Seasonal trends of light-saturated net photosynthesis and stomatal conductance of loblolly pine trees grown in contrasting environments of nutrition, water and carbon dioxide. Plant Cell Environ. 20, 558-568.

Myers, D. A., Thomas, R. B., DeLucia, E. H., 1999a. Photosynthetic responses of loblolly pine (*Pinus taeda*) needles to experimental reduction in sink demand. Tree Physiol. 19, 235-242.

Myers, D. A., Thomas, R. B., Delucia, E. H., 1999b. Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. Plant Cell Environ. 22, 473-481.

Nemeth, J. C., 1973. Dry matter production in young loblolly (*Pinus taeda* L) and slash pine (*Pinus elliottii* Engelm) plantations. Ecol. Monogr. 43, 21-41.

Niinemets, U., Kull, O., 1995. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: Variation in needle morphology. Tree Physiol. 15, 307-315.

Niinemets, U., Kull, O., Tenhunen, J. D., 1998. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiol. 18, 681-696.

Niinemets, U., Ellsworth, D. S., Lukjanova, A., Tobias, M., 2002. Dependence of needle architecture and chemical composition on canopy light availability in three North American *Pinus* species with contrasting needle length. Tree Physiol. 22, 747-761.

NOAA, 2002a, Climatography of the United States No. 81, Monthly Station Normals of Temperature, Precipitation, and Heating and Cooling, Degree Days 1971 – 2000, 41 Texas, National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service, National Climatic Data Center, Asheville, NC, p. 87.

NOAA, 2002b, Climatography of the United States No. 81, Monthly Station Normals of Temperature, Precipitation, and Heating and Cooling, Degree Days 1971 – 2000, 16 Louisiana, National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service, National Climatic Data Center, Asheville, NC, p. 25.

Norman, J. M., Welles, J. M., 1983. Radiative transfer in an array of canopies. Agron. J. 75, 481-488.

Norman, J. M., Arkebauer, T. J., 1991. Predicting canopy photosynthesis and light-use efficiency from leaf characteristics. In: Boote, K. J., Loomis, R. S. (Eds.), Modeling Crop Photosynthesis - From Biochemistry to Canopy. Crop Science Society of America, Inc., American Society of Agronomy, Inc., Madison, Wisconsin, pp. 75-94.

Norman, J. M., 1993. Scaling processes between leaf and canopy levels. In: Ehleringer, J. R., Field, C. B. (Eds.), Scaling Physiological Processes: Leaf to Globe. Academic Press, Inc., San Diego, CA, pp. 41-76.

Norman, J. M., Hesketh, J. D., 1980. Micrometeorological methods for predicting environmental effects on photosynthesis. In: Hesketh, J. D., Jones, J. W. (Eds.), Predicting Photosynthesis for Ecosystem Models. Vol. I. CRC Press Inc., Boca Raton, Florida, pp. 9-35.

Norman, J. M., 1980. Interfacing leaf and canopy light interception models. In: Hesketh, J. D., Jones, J. W. (Eds.), Predicting Photosynthesis for Ecosystem Models. Vol. II. CRC Press Inc., Boca Raton, Florida, pp. 49-57.

Oker-Blom, P., Kellomaki, S., 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: Comparison of random and grouping canopy models. Agric. Meteorol. 28, 143-155.

Oleksyn, J., Zytkowiak, R., Karolewski, P., Reich, P. B., Tjoelker, M. G., 2000. Genetic and environmental control of seasonal carbohydrate dynamics in trees of diverse *Pinus sylvestris* populations. Tree Physiol. 20, 837-847.

Ott, R. L., Longnecker, M., 2001. An Introduction to Statistical Methods and Data Analysis. Duxbury, Pacific Grove, CA, pp. 1152.

Pearcy, R. W., 1990. Sunflecks and photosynthesis in plant canopies. Annu. Rev. Plant Physiol. Plant Molec. Biol. 41, 421-453.

Pearcy, R. W., Muraoka, H., Valladares, F., 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. New Phytol. 166, 791-800.

Peterson, D. L., Spanner, M. A., Running, S. W., Teuber, K. B., 1987. Relationship of thematic mapper simulator data to leaf area index of temperate coniferous forests. Remote Sens. Environ. 22, 323-341.

Pierce, L. L., Running, S. W., 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. Ecology. 69, 1762-1767.

Pons, T. L., Schieving, F., Hirose, T., Werger, M. J. A., 1989. Optimization of leaf nitrogen allocation for canopy photosynthesis in *Lysimachia vulgaris*. In: Lambers, H., Cambridge, M. L., Konings, H., Pons, T. L. (Eds.), Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. SPB Academic Publishing, The Hague, The Netherlands, pp. 175-186.

Poorter, H., Evans, J. R., 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia. 116, 26-37.

Poorter, H., 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In: Lambers, H., Cambridge, M. L., Konings, H., Pons, T. L. (Eds.), Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. SPB Academic Publishing, The Hague, The Netherlands, pp. 45-68.

Poorter, H., Van der Werf, A., 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species In: Lambers, H., Poorter, H., Van Vuuren, M. M. I. (Eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, The Netherlands, pp. 309-336.

Poorter, H., Garnier, E., 1999. Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire, F. I., Valladares, F. (Eds.), Handbook of Functional Plant Ecology. Marcel Dekker, Inc., New York, pp. 81-120.

Reich, P. B., Walters, M. B., Ellsworth, D. S., 1997. From tropics to tundra: Global convergence in plant functioning. Proc. Natl. Acad. Sci. U. S. A. 94, 13730-13734.

Reich, P. B., Ellsworth, D. S., Walters, M. B., 1998. Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: Evidence from within and across species and functional groups. Funct. Ecol. 12, 948-958.

Reich, P. B., 1998. Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers, H., Poorter, H., Van Vuuren, M. M. I. (Eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, The Netherlands, pp. 467-487.

Roberts, S. D., 2002, Family differences in aboveground biomass allocation in loblolly pine. In: Outcalt, K. W. (Ed.), Proceedings of the Eleventh Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS–48., Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station, 72-76.

Roth, B. E., Jokela, E. J., Martin, T. A., Huber, D. A., White, T. L., 2007. Genotype x environment interactions in selected loblolly and slash pine plantations in the Southeastern United States. For. Ecol. Manage. 238, 175-188.

Running, S. W., Peterson, D. L., Spanner, M. A., Teuber, K. B., 1986. Remote sensing of coniferous forest leaf area. Ecology. 67, 273-276.

Ryan, M. G., Binkley, D., Fownes, J. H., 1997. Age-related decline in forest productivity: Pattern and process. Adv. Ecol. Res. 27, 213-262.

Samuelson, L., Stokes, T., Cooksey, T., McLemore, P., 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. Tree Physiol. 21, 369-376.

Samuelson, L. J., 2000. Effects of nitrogen on leaf physiology and growth of different families of loblolly and slash pine. New For. 19, 95-107.

Samuelson, L. J., Johnsen, K., Stokes, T., 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. For. Ecol. Manage. 192, 59-70.

Sands, P. J., 1996. Modelling canopy production. III. Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. Aust. J. Plant Physiol. 23, 103-114.

Schultz, R. P., 1997. Loblolly Pine: The Ecology and Culture of Loblolly Pine (*Pinus taeda* L.). Agriculture Handbook 713. U.S. Department of Agriculture, Forest Service, Washington, D.C., pp. 493.

Shiver, B., D., 2002. Loblolly versus slash pine growth and yield comparisons. In: Dickens, E. D., Barnett, J. P., Hubbard, W. G., Jokela, E. J. (Eds.), Slash Pine: Still Growing and Growing! Proceedings of the Slash Pine Symposium, Jekyll Island, Georgia, April 23–25, 2002. USDA For. Serv. Gen. Tech. Rep. SRS-76, pp. 45-49.

Shoulders, E., Tiarks, A. E., 1980. Predicting height and relative performance of major southern pines from rainfall, slope, and available soil moisture. For. Sci. 26, 437-447.

Stenberg, P., Kuuluvainen, T., Kellomaki, S., Grace, J. C., Jokela, E. J., Gholz, H. L., 1994. Crown structure, light interception and productivity of pine trees and stands. In: Gholz, H. L., Linder, S., McMurtrie, R. E. (Eds.), Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Ecol. Bull., Copenhagen, 43, pp. 20-34.

Stitt, M., 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14, 741-762.

Sword Sayer, M. A., Goelz, J. C. G., Chambers, J. L., Tang, Z., Dean, T. J., Haywood, J. D., Leduc, D. J., 2004. Long-term trends in loblolly pine productivity and stand characteristics in response to thinning and fertilization in the West Gulf region. For. Ecol. Manage. 192, 71-96.

Tang, Z. M., Chambers, J. L., Guddanti, S., Barnett, J. P., 1999. Thinning, fertilization, and crown position interact to control physiological responses of loblolly pine. Tree Physiol. 19, 87-94.

Tang, Z. M., Chambers, J. L., Sword, M. A., Barnett, J. P., 2003. Seasonal photosynthesis and water relations of juvenile loblolly pine relative to stand density and canopy position. Trees-Struct. Funct. 17, 424-430.

Teskey, R. O., Gholz, H. L., Cropper, W. P., 1994. Influence of climate and fertilization on net photosynthesis of mature slash pine. Tree Physiol. 14, 1215-1227.

Uemura, A., Harayama, H., Koike, N., Ishida, A., 2006. Coordination of crown structure, leaf plasticity and carbon gain within the crowns of three winter-deciduous mature trees. Tree Physiol. 26, 633-641.

Vose, J. M., 1988. Patterns of leaf area distribution within crowns of nitrogen- and phosphorus-fertilized loblolly pine trees. For. Sci. 34, 564-573.

Vose, J. M., Allen, H. L., 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. For. Sci. 34, 547-563.

Vose, J. M., Sullivan, N. H., Clinton, B. D., Bolstad, P. V., 1995. Vertical leaf area distribution, light transmittance, and application of the Beer-Lambert law in four mature hardwood stands in the southern Appalachians. Can. J. For. Res. 25, 1036-1043.

Vose, J. M., Dougherty, P. M., Long, J. N., Smith, F. W., Gholz, H. L., Curran, P. J., 1994. Factors influencing the amount and leaf distribution of leaf area of pine stands. In: Gholz, H. L., Linder, S., McMurtrie, R. E. (Eds.), Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Ecol. Bull., Copenhagen, 43, pp. 102-114.

Wang, Y. P., Jarvis, P. G., Benson, M. L., 1990. Two-dimensional needle-area density distribution within the crowns of *Pinus radiata*. For. Ecol. Manage. 32, 217-237.

Wang, Y. P., Jarvis, P. G., 1990a. Description and validation on an array model - MAESTRO. Agric. For. Meteorol. 51, 257-280.

Wang, Y. P., Jarvis, P. G., 1990b. Influence of crown structural properties on PAR absorption, photosynthesis and transpiration in Sitka spruce: Application of a model (MAESTRO). Tree Physiol. 7, 297-316.

Wang, Y. P., Jarvis, P. G., Taylor, C. M. A., 1991. PAR absorption and its relation to above-ground dry matter production of Sitka spruce. J. Appl. Ecol. 28, 547-560.

Waring, R. H., 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Adv. Ecol. Res. 13, 327-354.

Wellburn, A. R., 1994. The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. J. Plant Physiol. 144, 307-313.

Whitehead, D., Grace, J. C., Godfrey, M. J. S., 1990. Architectural distribution of foliage in individual *Pinus radiata* D. Don crowns and the effects of clumping on radiation interception. Tree Physiol. 7, 135-155.

Will, R. E., Barron, G. A., Colter Burkes, E., Shiver, B., Teskey, R. O., 2001. Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities. For. Ecol. Manage. 154, 155-163.

Will, R. E., Munger, G. T., Zhang, Y. J., Borders, B. E., 2002. Effects of annual fertilization and complete competition control on current annual increment, foliar development, and growth efficiency of different aged *Pinus taeda* stands. Can. J. For. Res. 32, 1728-1740.

Will, R. E., Narahari, N. V., Shiver, B. D., Teskey, R. O., 2005. Effects of planting density on canopy dynamics and stem growth for intensively managed loblolly pine stands. For. Ecol. Manage. 205, 29-41.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature. 428, 821-827.

Xiao, Y., Jokela, E. J., White, T. L., 2003a. Species differences in crown structure and growth performance of juvenile loblolly and slash pine. For. Ecol. Manage. 174, 295-313.

Xiao, Y., Jokela, E. J., White, T. L., 2003b. Growth and leaf nutrient responses of loblolly and slash pine families to intensive silvicultural management. For. Ecol. Manage. 183, 281-295.

Xu, M. G., Harrington, T. B., 1998. Foliage biomass distribution of loblolly pine as affected by tree dominance, crown size, and stand characteristics. Can. J. For. Res. 28, 887-892.

Zavitkovski, J., 1982. Characterization of light climate under canopies of intensively-cultured hybrid poplar plantations. Agric. Meteorol. 25, 245-255.

Zhang, S. S., Hennessey, T. C., Heinemann, R. A., 1997. Acclimation of loblolly pine (*Pinus taeda*) foliage to light intensity as related to leaf nitrogen availability. Can. J. For. Res. 27, 1032-1040.

APPENDIX A. TOTAL NON-STRUCTURAL CARBOHYDRATES IN RELATION TO CROWN POSITION IN LOBLOLLY AND SLASH PINE

At the Kirbyville site, the Lob 5 family had the lowest rates of photosynthesis at the middle and lower crown positions among the examined families (see Section 3). Photosynthesis may be inhibited by a feedback from a sink limitation, which is often accompanied by the accumulation of carbohydrates in leaves (Stitt, 1991; Lambers et al., 1998; Myers et al., 1999b). To test the hypothesis of photosynthesis feedback inhibition by foliar carbohydrates, we analyzed concentrations of total nonstructural carbohydrates (TNC) and soluble sugars on the same needles used for photosynthesis measurement or adjacent needles from the same needle cohort and branch sample for upper, middle, and lower crown positions of trees sampled at both the Kirbyville and DeRidder sites.

The TNC concentrations were determined with a modified method by Haissig and Dickson (1979) as described in Oleksyn et al. (2000). Sugars were extracted from oven-dried and ground tissue in methanol:chlorophorm:water (12:5:3 by volume) and the concentration of soluble sugars was determined colorimetrically with anthrone reagent at 625 nm. Starch in the tissue residue was gelled and hydrolyzed to glucose with amyloglucosidase for 24 hours. The sample was then mixed with glucose oxidase/peroxidase o-dianisidine dihydrochloride reagent, incubated for 15 minutes at 37 °C, and absorbance was read at 450 nm. Glucose concentrations in the samples were calculated from linear regression equations based on glucose standards. TNC concentrations are expressed on a leaf dry mass basis.

The pool of total nonstructural carbohydrates in leaves, when measured mid-season in 2006, was dominated by soluble sugars (Fig. A.1). Loblolly pine families had significantly higher TNC concentrations than the slash pine family (Fig. A.1), and starch concentrations were highest in needles of the Lob 1 family at both sites. The TNC concentrations were significantly affected by crown position. Soluble sugar concentrations were in general highest at the upper crown position, whereas starch concentration was highest in mid-crown foliage (Fig. A.1). The cultural treatment effect

was inconsistent among families for soluble carbohydrates at DeRidder, and among crown positions for both soluble sugars and starch at Kirbyville (significant interaction terms for family × treatment and treatment × crown position, respectively). These interactions, however, did not affect the general pattern of variability in TNC concentration presented in Fig. A.1. In general, we found no relationship between leaf-level photosynthesis and TNC concentrations, suggesting that feedback inhibition by carbohydrates was unlikely.

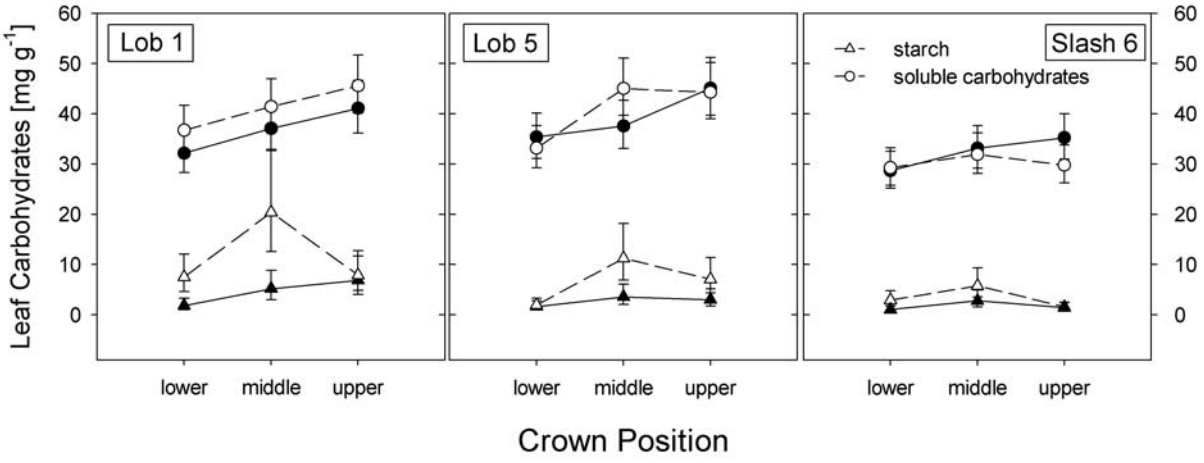

Figure A.1. Concentrations of total non-structural carbohydrates expressed as glucose equivalents within crowns of examined families of loblolly and slash pine in June 2006. Values were averaged across two cultural treatments (n = 18 for each point). Closed symbols with solid lines represent the Kirbyville site, and open symbols with dashed lines represent the DeRidder site. Error bars show 95% confidence intervals.

APPENDIX B. CARBON ISOTOPE DISCRIMINATION AND WATER-USE EFFICIENCY IN FAMILIES OF LOBLOLLY AND SLASH PINE

Increased water-use efficiency may be beneficial for plants growing in water-limited environments (Dudley, 1996). However, in the absence of water limitation or with use of practices that alleviate soil water shortage, e.g. control of competing vegetation, increased water-use efficiency may not confer a substantial growth advantage in managed pine plantations. Given the expected trade-off between increased water-use efficiency (WUE) and the efficient use of nitrogen in the photosynthetic apparatus (PNUE – photosynthetic nitrogen use efficiency; Field et al., 1983; DeLucia and Schlesinger, 1991), we hypothesized that differences in growth and biomass accumulation expressed among families would reflect differences in water-use efficiency. In environments not limited by water availability, aboveground productivity might be reduced by inherently increased water-use efficiency among families.

The photosynthetic enzyme Rubisco discriminates against the heavier stable carbon isotope – ^{13}C present in atmospheric CO_2, to varying degrees depending upon stomatal diffusive conductance. Therefore, the carbon isotopic composition of a leaf reflects its stomatal conductance during leaf development; and thus, may be used as a measure of time integrated water-use efficiency (Griffiths, 1991).

In February 2006, after the fourth growing season, needles were collected from all 7 families in three blocks at the Kirbyville and DeRidder sites for $\delta^{13}C$ determination. Needles were sampled from upper crowns on 10 trees per plot in each of three blocks at each site. Needles samples were oven-dried (70 °C) and powered in a ball mill. The analysis was completed in the Stable Isotope Facility at the University of California, Davis.

Silvicultural treatments did not affect significantly carbon isotope discrimination, but differences among families were significant at both sites (Table B.1). A correlation of $\delta^{13}C$ with annual aboveground growth increment at the DeRidder site (based on stand inventory data), was positive although statistically weak ($r = 0.34$, $P = 0.0263$),

indicating that families with higher WUE tended to produce more aboveground biomass. No relationship between $\delta^{13}C$ and aboveground growth increment was found for the Kirbyville site. For the loblolly pine families our hypothesis about decreasing aboveground growth with increasing WUE was not supported. The best growing family, Lob 5 had highest integrated WUE at both sites and the least productive loblolly family, Lob 7, had among the most negative values of $\delta^{13}C$, indicating lower WUE in this family. Slash pine differed from loblolly pine in WUE, as it ranked as the poorest-growing family, but ranked second for the highest WUE (Table B.1).

Table B.1. Mean values (s.e.) of ^{13}C isotope discrimination for loblolly and slash pine families during the fourth growing season at the DeRidder and Kirbyville experimental sites.

DeRidder			Kirbyville		
Family[1)]	**$\delta^{13}C$**		**Family**	**$\delta^{13}C$**	
Lob 5	-29.73[a]	(0.05)	Lob 5	-29.44[a]	(0.18)
Slash 6	-29.92[ab]	(0.14)	Slash 6	-29.89[ab]	(0.22)
Lob 2	-30.18[ab]	(0.21)	Lob 1	-29.96[ab]	(0.26)
Lob 4	-30.19[ab]	(0.17)	Lob 3	-30.09[ab]	(0.22)
Lob 1	-30.21[ab]	(0.22)	Lob 4	-30.11[b]	(0.12)
Lob 7	-30.34[ab]	(0.15)	Lob 7	-30.19[b]	(0.15)
Lob 3	-30.59[b]	(0.21)	Lob 2	-30.20[b]	(0.17)
mean	**-30.16**	**(0.07)**	**mean**	**-29.98**	**(0.08)**
Treatment[2)]			**Treatment**		
C	-30.19[a]	(0.12)	C	-30.15[a]	(0.09)
HI	-30.13[a]	(0.08)	HI	-29.81[a]	(0.11)
Source of Variation	**d.f.**	***P* > F**		**d.f.**	***P* > F**
treatment[3)]	1	0.3709		1	0.2676
family	6	**0.0300**		6	**0.0146**
fam x treatment	6	0.2061		6	0.3662

[1)] Families are rank-ordered based on $\delta^{13}C$ and hence, high to low water-use efficiency; values followed with the same superscript letters are not significantly different (family and treatment comparisons) at $\alpha = 0.05$ (Tukey-Kramer test). [2)]Silvicultural treatment comparison – C and HI refer to control and high intensity treatments, respectively. [3)]Block × cultural treatment with 2 d.f. was used as the error term for treatment effect, and the residual error with 24 d.f. for other effects.

APPENDIX C. SUPPLEMENTAL MATERIAL FOR LIGHT ABSORPTION MODELING

Table C.1. Parameter estimates (s.e.) of equations describing crown diameters, leaf biomass and branch biomass per tree at the DeRidder site.

	Crown Diameter Parameters[1)]							
Age / Family / Species	**crown diameters in *x* direction (perpendicular to planting beds)**				**crown diameters in *y* direction (parallel to planting beds)**			
3 years	**a**	**b**	**r^2**	***P***	**a**	**b**	**r^2**	***P***
Lob 1	0.86 (0.37)	0.20 (0.04)	0.37	< 0.0001	0.45 (0.25)	0.22 (0.03)	0.61	< 0.0001
Lob 5	-0.10 (0.34)	0.34 (0.04)	0.67	< 0.0001	0.21 (0.27)	0.27 (0.03)	0.69	< 0.0001
other Loblolly[2)]	0.37 (0.26)	0.27 (0.03)	0.52	< 0.0001	0.30 (0.19)	0.25 (0.02)	0.64	< 0.0001
Slash 6	0.40 (0.16)	0.19 (0.02)	0.69	< 0.0001	0.22 (0.16)	0.21 (0.02)	0.74	< 0.0001
4 years								
Lob 1	0.59 (0.41)	0.26 (0.04)	0.56	< 0.0001	1.42 (0.37)	0.13 (0.04)	0.27	0.0011
Lob 5	0.42 (0.54)	0.30 (0.05)	0.50	< 0.0001	1.11 (0.54)	0.18 (0.05)	0.27	0.0012
other Loblolly	0.44 (0.34)	0.29 (0.03)	0.53	< 0.0001	1.22 (0.32)	0.16 (0.03)	0.27	< 0.0001
Slash 6	0.17 (0.27)	0.24 (0.03)	0.71	< 0.0001	0.48 (0.37)	0.20 (0.04)	0.58	< 0.0001

	Foliage Biomass Parameters[3)]				
Age	**a**	**b**		**r^2**	***P***
2 years	-1.42 (0.14)	1.46	(0.11)	0.80	< 0.0001
3 years	-1.83 (0.10)	1.54	(0.05)	0.98	< 0.0001
4 years	-2.28 (0.21)	1.68	(0.10)	0.95	< 0.0001
6 years	-3.44 (0.46)	2.06	(0.18)	0.89	< 0.0001

	Branch Biomass Parameters[4)]							
Species	**a**	**b**		**c**		**r^2**	***P***	
Loblolly	85.84 (61.72)	2.25	(0.40)	0.34	(0.48)	0.95	< 0.0001	
Slash	103.40 (65.25)	2.40	(0.34)	0.39	(0.28)	0.97	< 0.0001	

[1)] Equation for crown diameter (CrD) in m: $CrD = a + bDBH$ was fitted for family/species across cultural treatments; DBH in cm.

[2)] Other loblolly denotes remaining loblolly pine families.

[3)] Equation for foliage biomass (FB) in kg: $lnFB = a + b\ lnDBH$ was fitted across species and cultural treatments; DBH in cm.

[4)] Equation for branch biomass (BB) in kg: $BB = a \times Ht\ (DBH)^b + c$ was fitted for age 2 and 6 years together across cultural treatments for each species; Ht and DBH in m.

Table C.2. Values (s.d.) of maximum electron transport rate (J_{max}; μmol m^{-2} s^{-1}) and maximum RuBP carboxylation (V_{cmax}; μmol m^{-2} s^{-1}) used in the model for canopy photosynthesis at the DeRidder site.

Species	Foliage Age Class	Parameter	Reference
		J_{max}	
Loblolly pine	current year	69.25 (7.46)	Maier et al., 2002; Myers et al., 1999a; Myers et al., 1999b
	previous year	74.42 (29.87)	Maier et al., 2002; Myers et al., 1999a; Myers et al., 1999b
Slash pine	current year	30.74 (6.41)	T.A. Martin, unpublished results
	previous year	36.88 (21.26)	T.A. Martin, unpublished results
		V_{cmax}	
Loblolly pine	current year	40.46 (6.98)	Maier et al., 2002; Myers et al., 1999a; Myers et al., 1999b
	previous year	35.18 (5.12)	Maier et al., 2002; Myers et al., 1999a; Myers et al., 1999b
Slash pine	current year	11.85 (4.49)	T.A. Martin, unpublished results
	previous year	13.47 (7.91)	T.A. Martin, unpublished results

Table C.3. Parameter estimates (s.e.) of equations describing leaf area per branch (equation 4.1, see Section 4) and proportions of current-year year foliage (equation 4.2) used in the simulations at the DeRidder site.

Species	Eq. 4.1 parameters			
	a	***b***	***c***	***d***
Loblolly	0.00012 (0.0001)	2.265 (0.117)	2.082 (0.691)	0.176 (0.086)
Slash	0.00016 (0.0001)	2.300 (0.123)	1.512 (1.109)	0.160 (0.156)
	Eq. 4.2 parameters			
	g	***h***	***i***	***j***
Loblolly	0.043 (0.036)	1.215 (0.046)	-0.420 (0.295)	0.420 (0.103)
Slash	-0.072 (0.085)	1.172 (0.076)	0.864 (0.457)	0.494 (0.099)

Table C.4. Median values of parameter estimates for the beta function (equation 4.4, see Section 4) describing the vertical leaf area distribution at the DeRidder experimental site.

Species / Cultural Treatment	Foliage Age Class	Parameters			r^2	*P*	N[1)]
		k	***m***	***n***			
Loblolly pine	current year	10.23	1.55	1.16	0.45	< 0.0001	12
Loblolly pine	previous year	18.69	0.80	3.56	0.59	< 0.0001	12
Slash pine	current year	4.42	1.06	0.60	0.41	< 0.0001	4
Slash pine	previous year	9.16	0.65	2.21	0.75	< 0.0001	3

[1)] N denotes number of trees used for development of each regression equation.

APPENDIX D. CROWN SHAPE DETERMINATION FOR LIGHT ABSORPTION MODELING

Crown shape, together with total leaf area and its distribution within the crown influences light interception in a forest canopy. The process-based model MAESTRA requires description of the outer crown shape profile for estimation of canopy light interception. We found family differences in crown shape at age 2 years (see Fig. 2.2). To test for the persistence of family differences at the onset of canopy closure at age 5 years, we examined crown shape in two selected families of loblolly pine (Lob 1- average growing, and Lob 5 – faster growing) after the fifth growing season in the field at the DeRidder site.

Crown diameters were measured in two directions, parallel and perpendicular to planting rows, at four points along the crown, divided into 0.25 increments of crown length from the base of the live crown. Two height poles with attached post levels were extended to each measurement position along the crown and the horizontal distance between poles was measured with a tape to the nearest 5 cm. In total we sampled 48 trees representing a range of tree sizes within family and silvicultural treatment (4 trees / 2 families / 2 treatments / 3 blocks).

Measured crown diameters were used to calculate a relative crown radius (relative to the maximum) at each crown position. Crown diameter was set to zero at the top of the crown. To describe the distribution of crown radii along the crown, we estimated parameters of a modified equation of Baldwin and Peterson (1997):

$$RCR = a \times \left(\frac{RHIC - 1}{RHIC + 1} \right) + b(1 - RHIC)^c \qquad \text{D. 1.}$$

where RCR is the relative crown radius, RHIC is the relative height in the crown and *a, b,* and *c* are the estimated parameters. Equation D.1 was fitted for each sampled tree ($r^2 > 0.91$, $P < 0.0001$). Mean fits for family within silvicultural treatment are shown in Fig. D.1.

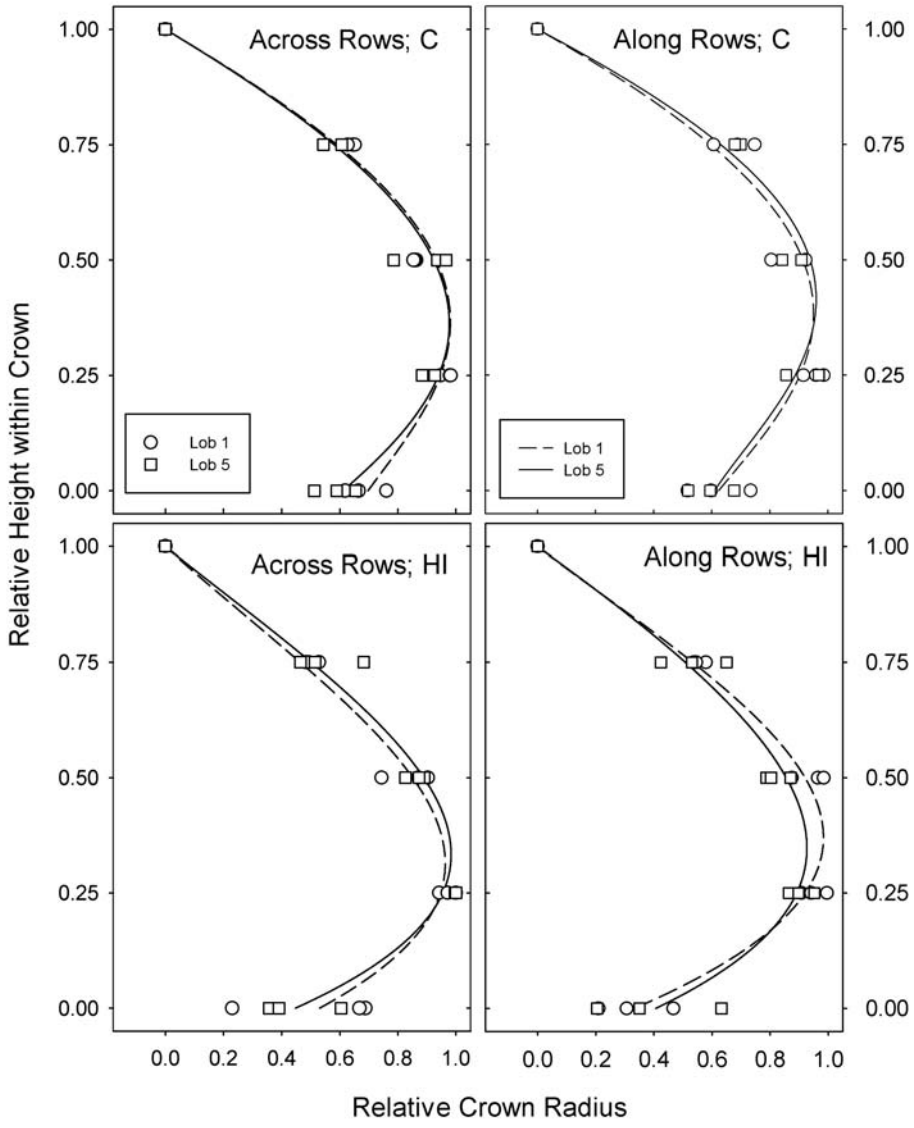

Figure D.1. The outer crown shape profiles in two loblolly pine families in two silvicultural treatments at the DeRidder site after the fifth growing season. Each symbol represents a plot mean based on four trees. Lines represent fits with equation D.1; $r^2 > 0.91$ for the Lob 1 family (dashed line) and $r^2 > 0.92$ for the Lob 5 family; all $P < 0.0001$. The C and HI denote control and high intensity treatment, respectively.

After the fifth growing season, crown shapes of both sampled loblolly pine families were similar. Crown radii tended to be relatively smaller at the canopy base in

the HI than in the control treatment, but the distribution of crown radii peaked between 0.25 and 0.5 of relative crown height in both treatments and families (Fig. D.1). Based on these findings, we used an ellipsoidal crown shape in simulations of canopy light absorption in the MAESTRA model (see Section 4).

VITA

Daniel Jozef Chmura received his Master of Science degree in Forestry from The August Cieszkowski Agricultural University of Poznan, Poland, in 1998. He entered the Texas A&M University graduate program in Forestry in August 2004, after a nine-month Fulbright scholarship. During this time he published two articles in peer-reviewed journals, and gave six presentations at scientific and professional meetings. He is the recipient of the 2007 Critchfield Award for the best presentation by a graduate student at the Joint Meeting of the Southern Forest Tree Improvement Conference and the Western Forest Genetics Association in Galveston, Texas. His research interests include genetic and physiological determinants of variation in productivity of forest trees, tree improvement and quantitative genetics.

Mr. Chmura may be reached at the Department of Ecosystem Science and Management, Texas A&M University, 2138 TAMU, College Station, TX 77843-2138, or at the Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035, Kornik, Poland.

e-mail addresses: djchmura@tamu.edu, djchmura@poczta.onet.pl